EVOLUTION AND GEOGRAPHY: THE BIOGEOGRAPHIC HISTORY OF SOUTH AMERICAN LAND MAMMALS[1]

Rosendo Pascual[2]

ABSTRACT

Based on the unequaled southern Late Cretaceous–Cenozoic record, the history of South American land mammals is divisible into two major episodes we term the Gondwanan Episode and the South American Episode. The former episode is distinguished by the northern and central Patagonian Argentinian record, while the latter is mostly based on the extra-Patagonian Argentinian record. The Gondwanan Episode is so termed because it is exclusively represented by endemic mammals of Gondwanan origin, i.e., Mesozoic lineages. In contrast, the South American Episode is almost exclusively distinguished by endemic Therian mammals whose ancestors emigrated from the Laurasian North American Continent.

These two major, successive, and for some time superimposed episodes are the result of the geologic history of the South American Plate. (1) This plate was part of the Gondwana Supercontinent until about 120 millions of years before Present (mybP), when it began to separate and drifted westward (but always south and relatively near the North American Plate). Until about 30 mybP it was connected to Western Antarctica, and through it to most of the Eastern Gondwanan continents. (2) By approximately 125 mybP, Donnelly's "Flood Basalt" was initiated. After its cessation by 85 mybP a variety of compressive tectonic features around the Caribbean began, i.e., subduction and island arcs or continental margin magmatism. These features probably permitted the first known inter-American exchange of tetrapods, dinosaurs such as Hadrosauridae from the rising North American continent and Titanosauridae Saltasaurinae from the South American continent. Probably by the latest Cretaceous these geologic features also permitted the immigration of the first Therian, which gave rise to the native South American land mammals. (3) The geologic definition of southern Central America is the last and most important phenomenon related to the final connection of both Americas. By 12 mybP the submarine connection of Central America with South America began, and subsequent volcanic island arcs permitted the beginning of The Great American Biotic Interchange.

According to the Patagonian record, the absence of tribosphenic mammals and the total extinction of the endemic non- and pre-tribosphenic mammals are the most outstanding events characterizing the Gondwanan Episode. Up to the beginning of the South American Episode (early Paleocene), few Gondwanan lineages of mammals (a native Gondwanatheria and an endemic Dryolestoid) survived in the South American continent; another related Gondwanatheria taxon survived up to the Late Eocene in Western Antarctica. These Gondwanan survivors lived together with the first, but advanced, immigrant Therian that initiated the South American Episode. Although not conclusively demonstrated, there are some suggestions that this superposition began earlier, probably by the pre-Campanian Cretaceous. The history of endemic Therian mammals characterizing the South American Episode began to be known in 1948 thanks to the efforts of the Ameghinos and G. G. Simpson. These represented the only known higher taxa until 1985 when Bonaparte recorded the first non-therian Gondwanan lineages in Late Cretaceous (Campanian) Patagonian beds. Successive authors contributed to this history, ratifying Simpson's statement that the South American Cenozoic mammal evolution was episodic. Thus, the most characteristic geobiotic features of the two major episodes are based almost exclusively on the most eloquent Campanian-Quaternary Argentinian record.

Key words: South America, land mammals, evolution, geography, Gondwanan Episode, South American Episode.

RESUMEN

De acuerdo a registros sin iguales del Cretácico–Cenozoico tardío meridional, la historia de los mamíferos terrestres suramericanos se puede dividir en dos episodios importantes que llamamos el Episodio de Gondwana y el Episodio Suramericano. El primer episodio se distingue por el registro argentino patagónico del norte y centro, mientras que el segundo se basa sobre todo en el registro extra argentino patagónico. El Episodio de Gondwana es así llamado porque está representado

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[1] I extend special thanks to Peter Raven for his invitation to be one of the speakers of this symposium. To be selected among such prominent scientists is a great honor, especially by so distinguished an investigator as the Director of the well-known Missouri Botanical Garden. I would like to address a very special acknowledgment to Alan Graham, as well as to Mick Richardson and Victoria Hollowell, whose assistance was not only uncommon but also decisive in making our stay a real pleasure. Without exception, we are also indebted to all the organizers of this pleasant and successful symposium. Special thanks to Olga M. Montiel. Most of the figures were masterfully designed by Agustin Viñas; others by Laura Zampatti, Carlos Vildoso Morales, and Marcela Tomeo. As always, Laura Zampatti contributed to the composition of the paper, suggesting invaluable syntactic ideas. Constructive criticisms and suggestions were made by the referees, Richard Cifelli and Guillermo Rougier, as well by Victoria C. Hollowell (Scientific Editor) and Sophia R. Balcomb (editor); all their suggestions and corrections, without any question, improved this paper. It is obvious that English is not my native language. Hence, I left quite a job for my friend R. Cifelli and the editors!! To all of them, I am very grateful.

[2] Departamento Paleontología Vertebrados, Museo de La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina. ropascua@museo.fcnym.unlp.edu.ar

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exclusivamente por los mamíferos endémicos de origen gondwánico, i.e., linajes mesozoicos. En contraste, el Episodio Suramericano se distingue casi exclusivamente por mamíferos terios endémicos cuyos antepasados emigraron del continente laurásico norteamericano.

Estos dos episodios importantes, sucesivos y por cierto tiempo sobrepuestos son el resultado de la historia geológica de la placa suramericana. (1) Esta placa formaba parte del supercontinente de Gondwana hasta cerca de 120 maap, cuando comenzó a separarse y desplazarse hacia el oeste (pero siempre al sur y relativamente cerca de la placa norteamericana). Hasta hace cerca de 30 maap estuvo conectada a Antártica occidental, y a través de esta a la mayoría de los continentes gondwánicos orientales. (2) Alrededor de 125 maap, empezó la "inundación basáltica" de Donnelly. Después de su cesación hace 85 maap, comenzó una variedad de características tectónicas compresivas alrededor del Caribe, i.e., arcos de islas y subducción o magmatismo marginal continental. Estas características probablemente permitieron el primer intercambio interamericano conocido de tetrápodos, dinosaurios tales como Hadrosauridae del continente norteamericano en levantamiento y Titanosauridae Saltasaurinae del continente suramericano. Probablemente hacia fines del Cretácico estas características geológicas también permitieron la migración del primer terio, que dio origen a los mamíferos terrestres suramericanos. (3) La definición geológica del sur de América Central es el último y más importante fenómeno relacionado con la conexión final de ambas Américas. Hace 12 maap comenzó la conexión submarina de América Central y del Sur, y subsecuentes arcos de isla volcánicos permitieron el inicio del Gran Intercambio Biótico Americano.

Según el registro patagónico, la ausencia de mamíferos tribosfénicos y la extinción total de los mamíferos endémicos no- y pre-tribosfénicos son los acontecimientos más excepcionales que caracterizan el Episodio de Gondwana. Hasta principio del Episodio Suramericano (Paleocene temprano), pocos linajes gondwánicos de mamíferos (un Gondwanaterio nativo y un Dryolestoide endémico) sobrevivieron en el continente suramericano; otro taxón Gondwanaterio relacionado sobrevivió hasta el Eoceno tardío en Antártica occidental. Estos sobrevivientes de Gondwana vivieron juntos con el primer, pero avanzado, inmigrante terio que inició el Episodio Suramericano. Aunque no se ha demostrado en forma concluyente, hay algunas sugerencias de que esta superposición comenzó antes, probablemente por el Cretácico pre-Campaniano. La historia de los mamíferos terios endémicos que caracterizan el Episodio Suramericano se empezó a conocer en 1948 gracias a los esfuerzos de los Ameghinos y G. G. Simpson. Estos representaban los únicos taxones avanzados conocidos hasta 1985 cuando Bonaparte registró los primeros linajes no terios de Gondwana en depósitos patagónicos del Cretácico tardío (Campaniano). Autores posteriores contribuyeron a esta historia, ratificando las afirmaciones de Simpson que la evolución de los mamíferos suramericanos cenozoicos fue episódica. Así, las características geobióticas más distintivas de los dos episodios más importantes se basan casi exclusivamente en el más elocuente registro argentino del Campaniano-Cuaternario.

INTRODUCTION AND METHODS

The purpose of this paper is to analyze the first order geologic-geographic phenomena, and the related climatic-environmental changes, that governed the evolutionary history of land mammals recorded to date in the present Patagonian region of the South American continent. This is not a mere analysis of the systematic changes that successively occurred in the mammal communities during the short time that South America was an island continent (a short time because, according to Zachos et al. (2001), the island continent began to be totally isolated from ca. 30 mybP (Fig. 1), not from the beginning of the Cenozoic as Simpson (e.g., 1980) and followers thought). While the history of South American land mammals has been extensively treated, virtually all such treatments were published before recognition of the recently discovered Gondwanan mammals (Campanian and the last earliest Paleocene representatives). Thus, this paper emphasizes the distinct history of the Gondwanan mammal communities with respect to the relatively well-known Cenozoic and Recent South American mammal communities.

The history of South American mammals is something like two histories in one. Within the framework of plate tectonics, varying paleogeographic states divided the history of land mammals recorded in the southern South American continent into two distinct episodes: the Gondwanan Episode and the South American Episode. In fact, the tribosphenic mammals recorded in Late Jurassic beds of the present South American continent (Fig. 2), as well as an advanced pretribosphenic mammal recorded in Early Cretaceous beds (Fig. 3), both in Patagonia, correspond to two somewhat distinct geographical situations when South America was an emerging continent still not well separated from the African continent. Thus, the Gondwanan and South American Episodes are the only two presently well-established major episodes in the history of South American mammals. With that in mind, I will not detail the trends and features of the successive mammal communities as, for example, was done following the previously recognized faunistic cycles (Pascual et al., 1996). For example, within the South American Episode I will only point out the main events that characterize what Stehli and Webb (1985) distinguished as The Great American Biotic Interchange,

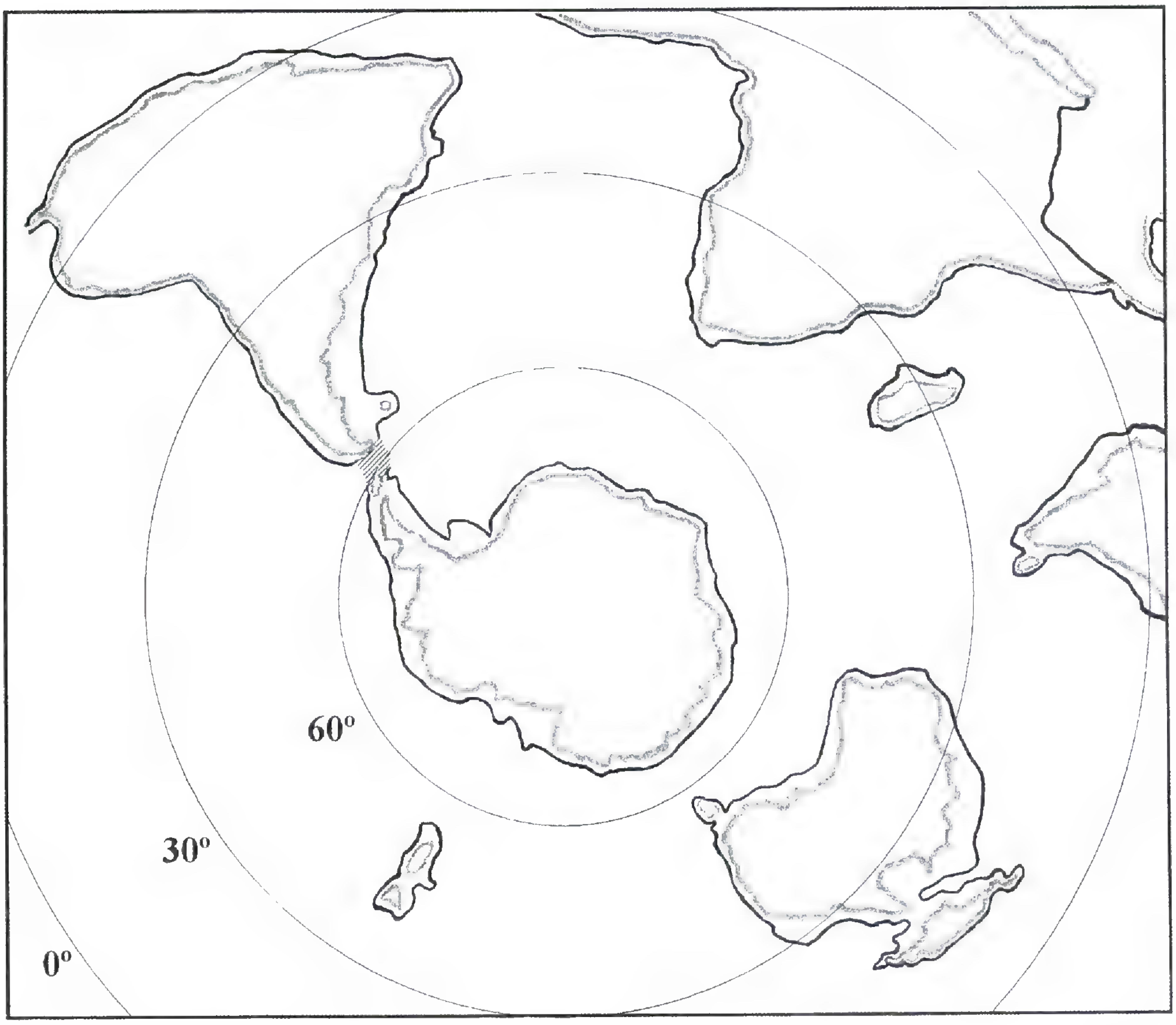


Figure 1. The geographic situation of South America and Antarctica 30 mybP. According to Zachos et al. (2001), these continents were totally separated by this time, thus beginning the transcendental isolation of the South American continent. Land masses 30 mybP are outlined in black.

which has been aptly developed by Webb (2006 this issue) and, independently, but complementarily, by Coates (2003).

As Simpson (1950, 1980) correctly indicated, the history of South American mammals was episodic and divisible into significant intervals of compositional changes, and thus provides the biochronological framework in which to understand their evolution and the evolution of their environments. Because of this, most North and South American paleomammalogists use the Land Mammal Age (LMA)—in our case, the South American Land Mammal Age (SALMA)—as the basic biochronological unit (but see Cione & Tonni, 1995). "Mammal Ages were intended to represent divisions of the Cenozoic, based on characteristic groups of fossil mammals whose temporal relationships and overall stage of evolution were thought to be indicative of a particular interval of geologic time… attention was given to first and last occurrences, 'index fossils' were noted, and characterizing assemblages were listed" (Woodburne, 1987: 1).

The hierarchical arrangement of the SALMAs reveals clusters that represent evolutionary episodes of mammal communities, not only taxonomically, but, more importantly, according to ecological modifications. Ortiz-Jaureguizar (1986) performed a multivariate analysis of similarity among SALMAs, a method that was subsequently revisited and updated by Pascual & Ortiz-Jaureguizar (1990) and Pascual et al. (1996). As Ortiz-Jaureguizar (1986) did, these latter authors used SALMAs as operational taxonomic units (OTUs) and families of the Late Cretaceous and Cenozoic Land-Mammal Ages as "characters." They were able to recognize four hierarchical ranks of SALMA organization, distinguished as Faunistic Units; from lower to higher these were Faunistic Subcycles, Faunistic Cycles, Faunistic Supercyles, and Faunistic Megacycles (Table 1). Major changes observed among mammal communities (Pascual & Ortiz-Jaureguizar, 1990; Pascual et al., 1996; Pascual, 2001) appear to be concomitantly related to major environmental changes, apparently correlated with

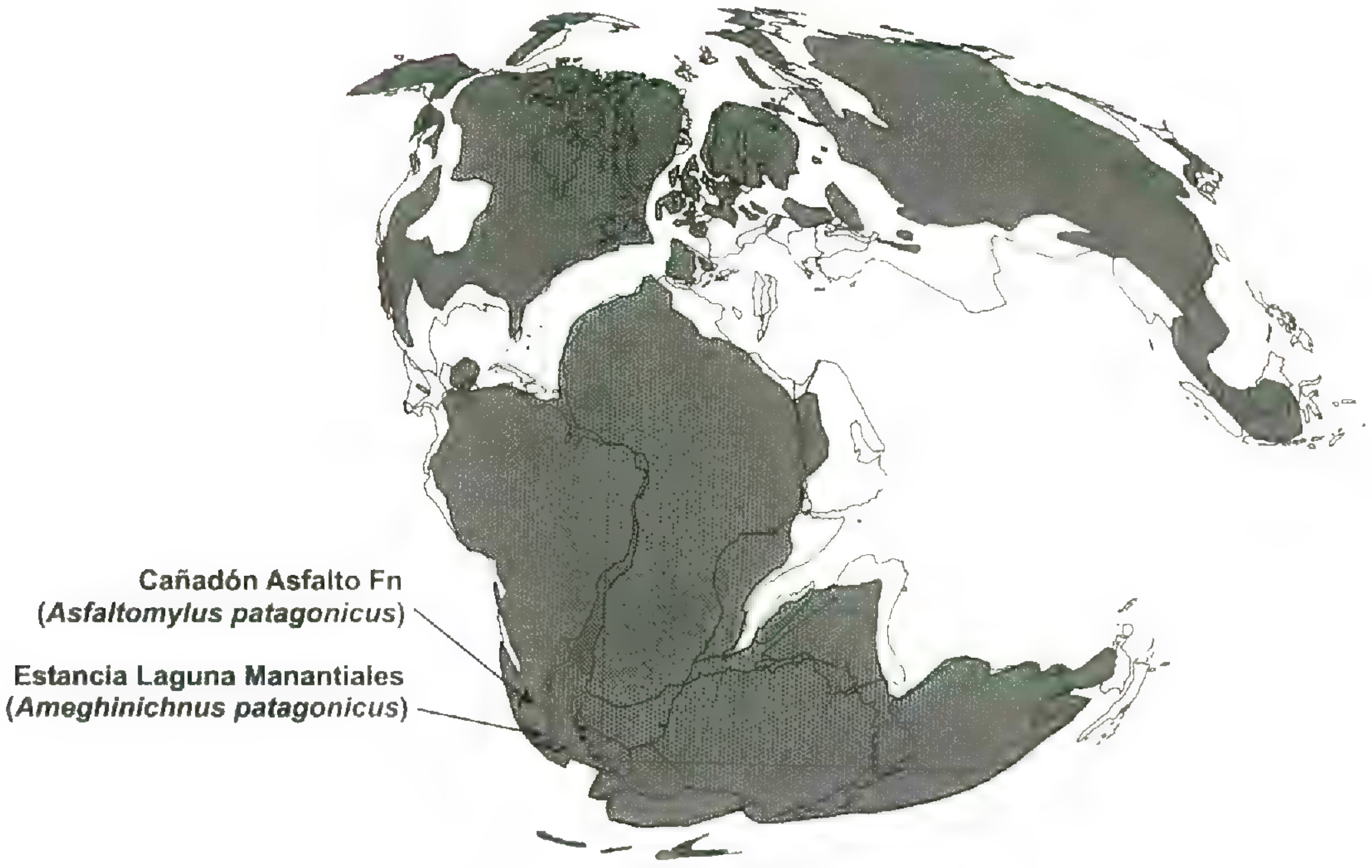

Cañadón Asfalto Fn
(*Asfaltomylus patagonicus*)
Estancia Laguna Manantiales
(*Ameghinichnus patagonicus*)

Figure 2. The paleogeographic situation of the South American continent by the end of the Jurassic, 155 mybP, i.e., still connected to the remaining Gondwanan continents (*fide* Smith et al., 1994). This apparently explains the persistence of Eutherian mammals in what was going to be the Patagonian territory, and their absence during the Patagonian Late Cretaceous Gondwanan Episode. *Asfaltomylus patagonicus* Rauhut, Martin, Ortiz-Jaureguizar & Puerta, 2002 is a Late Jurassic tribosphenic mammal found in Patagonia (Chubut), and *Ameghinichnus patagonicus* Casamiquela, 1961 is a Late Jurassic ichnita of a supposed Pantotheria, also from Patagonia (Santa Cruz). Grey shading represents land masses 155 mybP. (Modified from Smith et al., 1994; reprinted with the permission of Cambridge University Press.)

worldwide diastrophic phenomena. We use diastrophic phenomena in its most comprehensive sense including the fragmentation and drifting of continents, sea level changes, etc. We recently (Pascual & Ortiz-Jaureguizar, 1992; Pascual et al., 1996; Pascual & Ortiz-Jaureguizar, in press) also applied this biochronological classification to Late Cretaceous mammal communities from Patagonia known to date (Scillato-Yané & Pascual, 1984, 1985; Bonaparte et al., 1993), including the recently discovered, earliest mammal-bearing Paleocene formation that documents the last known Gondwanan survivors. To avoid repetition, and

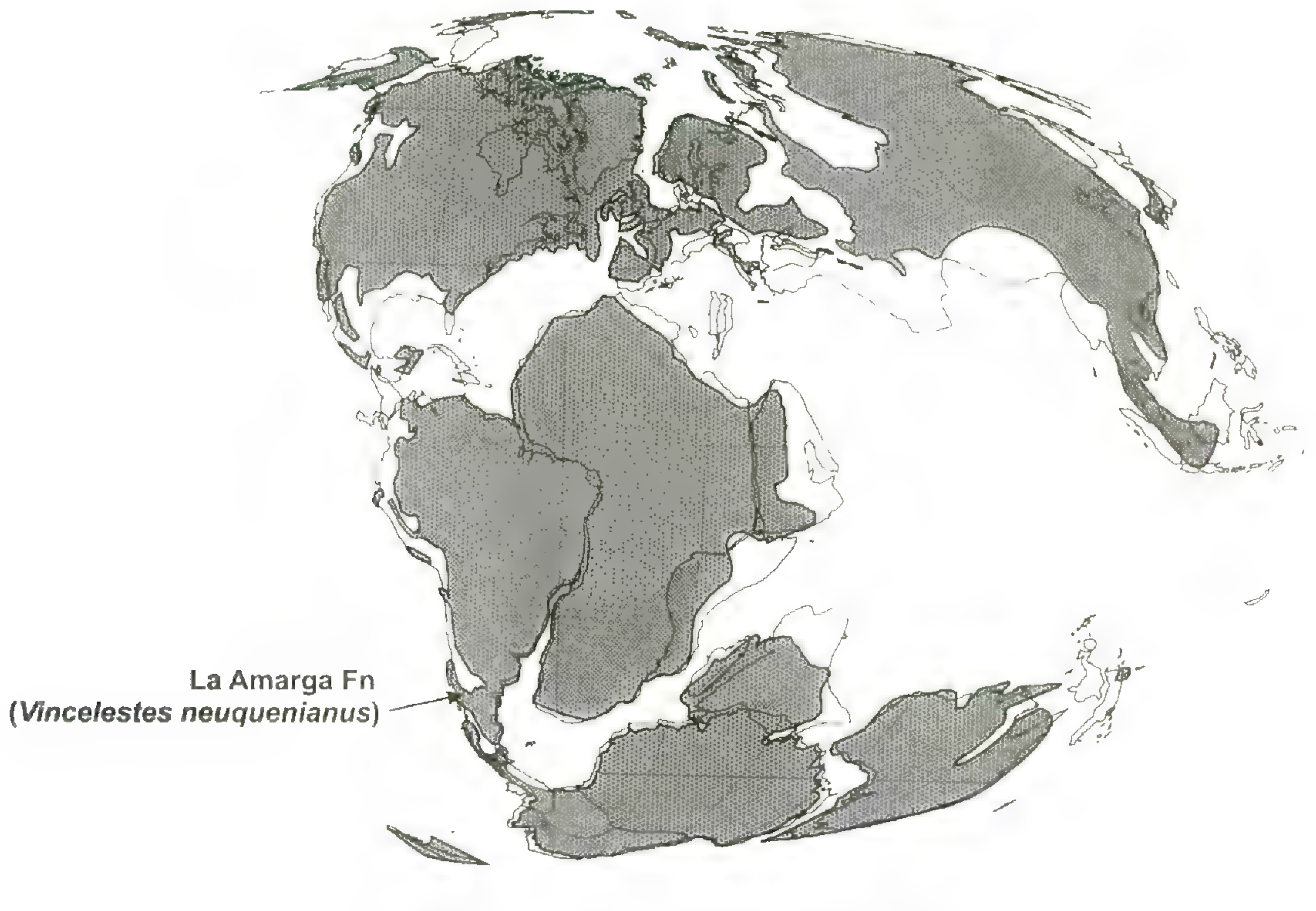
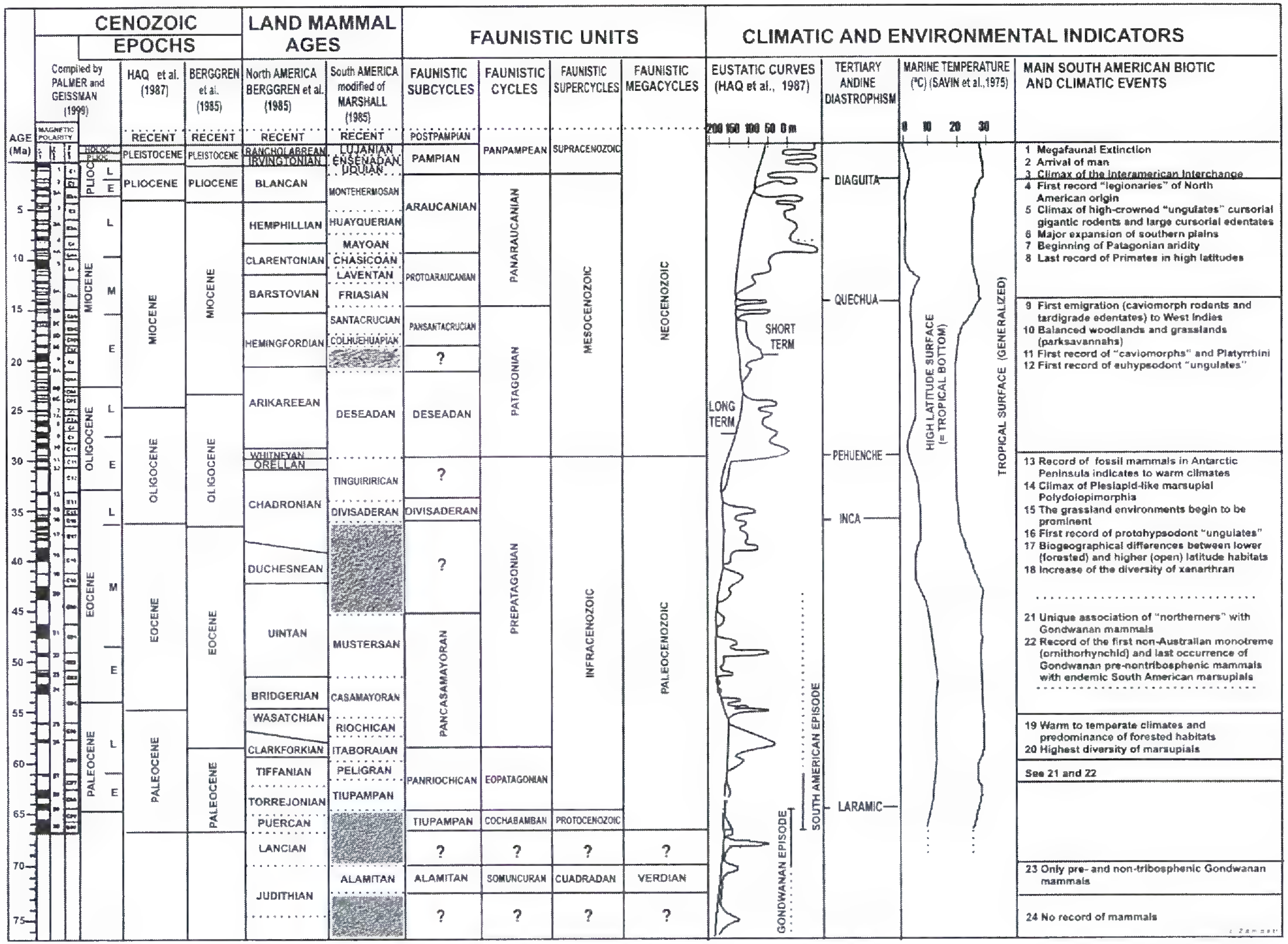


Figure 3. The primordial South American and African continents had somewhat drifted apart but were still tenuously connected by 135 mybP. This explains why the Early Cretaceous *Vincelestes neuquenianus*, recorded in the northwestern Patagonian bed of La Amarga Formation, is not part of the Gondwanan Episode. Grey shading represents land masses 135 mybP. (Modified from Smith et al., 1994; reprinted with the permission of Cambridge University Press.)

Table 1. Land-mammal Ages: dates, faunistic units, and the main climatic and environmental indicators.


CENOZOIC
EPOCHS
LAND MAMMAL AGES
FAUNISTIC UNITS
CLIMATIC AND ENVIRONMENTAL INDICATORS
AGE (Ma)
MAGNETIC POLARITY
Compiled by PALMER and GEISSMAN (1999)
HAQ et al. (1987)
BERGGREN et al. (1985)
North AMERICA BERGGREN et al. (1985)
South AMERICA modified of MARSHALL (1985)
FAUNISTIC SUBCYCLES
FAUNISTIC CYCLES
FAUNISTIC SUPERCYCLES
FAUNISTIC MEGACYCLES
EUSTATIC CURVES (HAQ et al., 1987)
TERTIARY ANDINE DIASTROPHISM
MARINE TEMPERATURE (°C) (SAVIN et al.,1975)
MAIN SOUTH AMERICAN BIOTIC AND CLIMATIC EVENTS
5
10
15
20
25
30
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40
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60
65
70
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HOLOC.
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EOCENE
PALEOCENE
RECENT
RANCHOLABREAN
IRVINGTONIAN
BLANCAN
HEMPHILLIAN
CLARENTONIAN
BARSTOVIAN
HEMINGFORDIAN
ARIKAREEAN
WHITNEYAN
ORELLAN
CHADRONIAN
DUCHESNEAN
UINTAN
BRIDGERIAN
WASATCHIAN
CLARKFORKIAN
TIFFANIAN
TORREJONIAN
PUERCAN
LANCIAN
JUDITHIAN
RECENT
LUJANIAN
ENSENADAN
UQUIAN
MONTEHERMOSAN
HUAYQUERIAN
MAYOAN
CHASICOAN
LAVENTAN
FRIASIAN
SANTACRUCIAN
COLHUEHUAPIAN
DESEADAN
TINGUIRIRICAN
DIVISADERAN
MUSTERSAN
CASAMAYORAN
RIOCHICAN
ITABORAIAN
PELIGRAN
TIUPAMPAN
ALAMITAN
POSTPAMPIAN
PAMPIAN
ARAUCANIAN
PROTOARAUCANIAN
PANSANTACRUCIAN
?
DESEADAN
?
DIVISADERAN
?
PANCASAMAYORAN
PANRIOCHICAN
TIUPAMPAN
?
ALAMITAN
?
PANPAMPEAN
PANARAUCANIAN
PATAGONIAN
PREPATAGONIAN
EOPATAGONIAN
COCHABAMBAN
?
SOMUNCURAN
?
SUPRACENOZOIC
MESOCENOZOIC
INFRACENOZOIC
PROTOCENOZOIC
?
CUADRADAN
?
NEOCENOZOIC
PALEOCENOZOIC
?
VERDIAN
?
200 150 100 50 0 m
SHORT TERM
LONG TERM
GONDWANAN EPISODE
SOUTH AMERICAN EPISODE
DIAGUITA
QUECHUA
PEHUENCHE
INCA
LARAMIC
0 10 20 30
HIGH LATITUDE SURFACE (= TROPICAL BOTTOM)
TROPICAL SURFACE (GENERALIZED)
L. Zamaloa

1 Megafaunal Extinction
2 Arrival of man
3 Climax of the interamerican Interchange

4 First record "legionaries" of North American origin
5 Climax of high-crowned "ungulates" cursorial gigantic rodents and large cursorial edentates
6 Major expansion of southern plains
7 Beginning of Patagonian aridity
8 Last record of Primates in high latitudes

9 First emigration (caviomorph rodents and tardigrade edentates) to West Indies
10 Balanced woodlands and grasslands (parksavannahs)
11 First record of "caviomorphs" and Platyrrhini
12 First record of euhypsodont "ungulates"

13 Record of fossil mammals in Antarctic Peninsula indicates to warm climates
14 Climax of Plesiapid-like marsupial Polydolopimorphia
15 The grassland environments begin to be prominent
16 First record of protohypsodont "ungulates"
17 Biogeographical differences between lower (forested) and higher (open) latitude habitats
18 Increase of the diversity of xenarthran

21 Unique association of "northerners" with Gondwanan mammals
22 Record of the first non-Australian monotreme (ornithorhynchid) and last occurrence of Gondwanan pre-nontribosphenic mammals with endemic South American marsupials

19 Warm to temperate climates and predominance of forested habitats
20 Highest diversity of marsupials

See 21 and 22

23 Only pre- and non-tribosphenic Gondwanan mammals

24 No record of mammals

to provide a synopsis of essential features, I herein summarize the main evolutionary events that mark the history of South American mammals according to the higher Faunistic Cycles (Table 1), although in some cases transcendental events punctuate these inclusive Faunistic Cycles and Subcycles.

ANTECEDENTS

None of the three of the most outstanding connaisseurs of the South American extinct and extant land mammals, Carlos and Florentino Ameghinos (see Simpson, 1948: 19–26) and G. G. Simpson (1980), were aware of the recently incorporated South American Mesozoic mammals. However, F. Ameghino and Simpson, based on distinct, supposedly positive, evidence, did consider that they knew them. For example, C. Ameghinos found dinosaur-like teeth associated with mammals of Casamayoran age (early Eocene) in central Patagonia (Ameghino, 1906). F. Ameghino interpreted these zyphodont teeth as pertaining to a carnivorous dinosaur (Ameghino, 1906). Simpson (1932, 1933, and particularly, 1937a, 1937b), using relatively complete, and different, remains, demonstrated that these teeth pertained to a curious and unique terrestrial crocodilian species, which he named *Sebecus icaeorhinus* Simpson and included in a new peculiar infraorder he named Sebecosuchia (Simpson, 1937a). In 1946, E. H. Colbert accepted Simpson's request to finish his study and published a monographic study on the best specimens collected by Simpson and his staff of the American Museum of Natural History of New York (Colbert, 1946). Colbert corroborated both the crocodilian nature of this specimen and that it was stratigraphically associated with mammals of Eocene age (Casamayoran SALMA). However, even at the time he studied those crocodilian remains, he considered the relationships of this new crocodile to be questionable (Colbert, 1946; see also the conclusions of Gasparini, 1984).

Of course Simpson's papers, and Colbert's conclusive paper, were unknown to F. Ameghino, who died in 1911 thinking that supposedly carnivorous dinosaurs lived in South America during the Cretaceous and were associated with more advanced mammals than were known from anywhere else in the world. Consequently, he regarded these mammal-bearing beds with supposedly carnivorous dinosaur teeth as Cretaceous in age, whereas Simpson later considered these beds to be Eocene in age (Simpson, 1937a), representing the Casamayoran SALMA (Table 1).

The transcending point is that, on this basis, F. Ameghino built a chronological scale that was too old and which he used as standard not only for South American land mammal-bearing beds but also for all related lithostratigraphical units (Ameghino, 1906). This was his *péché originale*, which so negatively influenced his otherwise extraordinary work. This transcendent error produced an almost universal reaction against him, especially when he suggestively named monkey (Ceboidea) remains, found in what he took as early Eocene beds of Patagonia, *Homunculus patagonicus* Ameghino (Ameghino, 1891). About this species he wrote "...es un mono de caracteres muy elevados, y lo considero como formando parte de la línea que conduce al hombre y a los antropomorfos" (Ameghino, 1891: 291).

Simpson (1980), in turn, accepted the Cretaceous age of the mammal-bearing Umayo Formation discovered by the French paleontologist B. Sigé (Grambast et al., 1967; Sigé, 1972) in the southern Peruvian Andes. These French paleontologists correlated this formation with the marine Vilquechico Formation, exposed further to the north and undoubtedly Cretaceous in age, and wrongly used the same name. The mammals collected in the Umayo Formation were later demonstrated to be early Paleocene, not Cretaceous, in age (Crochet, 1979). What Simpson (1980: 39) expressed about these Peruvian mammals is quite instructive: "... it would have been expected that mammals like these would occur in the Cretaceous of South America." Simpson did not admit that non-tribosphenic and pre-tribosphenic mammals were inhabitants, at least, during the Late Cretaceous of the South American continent, and by extension—considering his non-acceptance of the Plate Tectonic rationale—that what we presently accept as the Gondwana supercontinent had no such pre-Cenozoic mammals as inhabitants.

It has to be remarked that what was known by Simpson (Simpson, 1980) as the "curious history" of South American mammals was based only on the endemic Cenozoic mammals, the majority of which descended from Laurasian mammal immigrants from the primordial North American continent. No Gondwanan mammal was known until the 1980s, when Bonaparte and staff (Bonaparte et al., 1984; Bonaparte & Soria, 1985; Bonaparte, 1986a, 1986b, 1988, 1990, 1996) found the first unquestionable Late Cretaceous mammals, and simultaneously Pascual and staff (e.g., Scillato-Yané & Pascual, 1984, 1985) found the last relictual representatives, also in Patagonia but in beds of early Paleocene age. None of the relatively well known Cenozoic and living mammals show features indicating a Gondwanan ancestry.

The Gondwanan mammals completely disappeared by the early Paleocene, at least in Southern South America, in contrast to what happened, for example, with the Monotremata in Australia. Probable Gond-

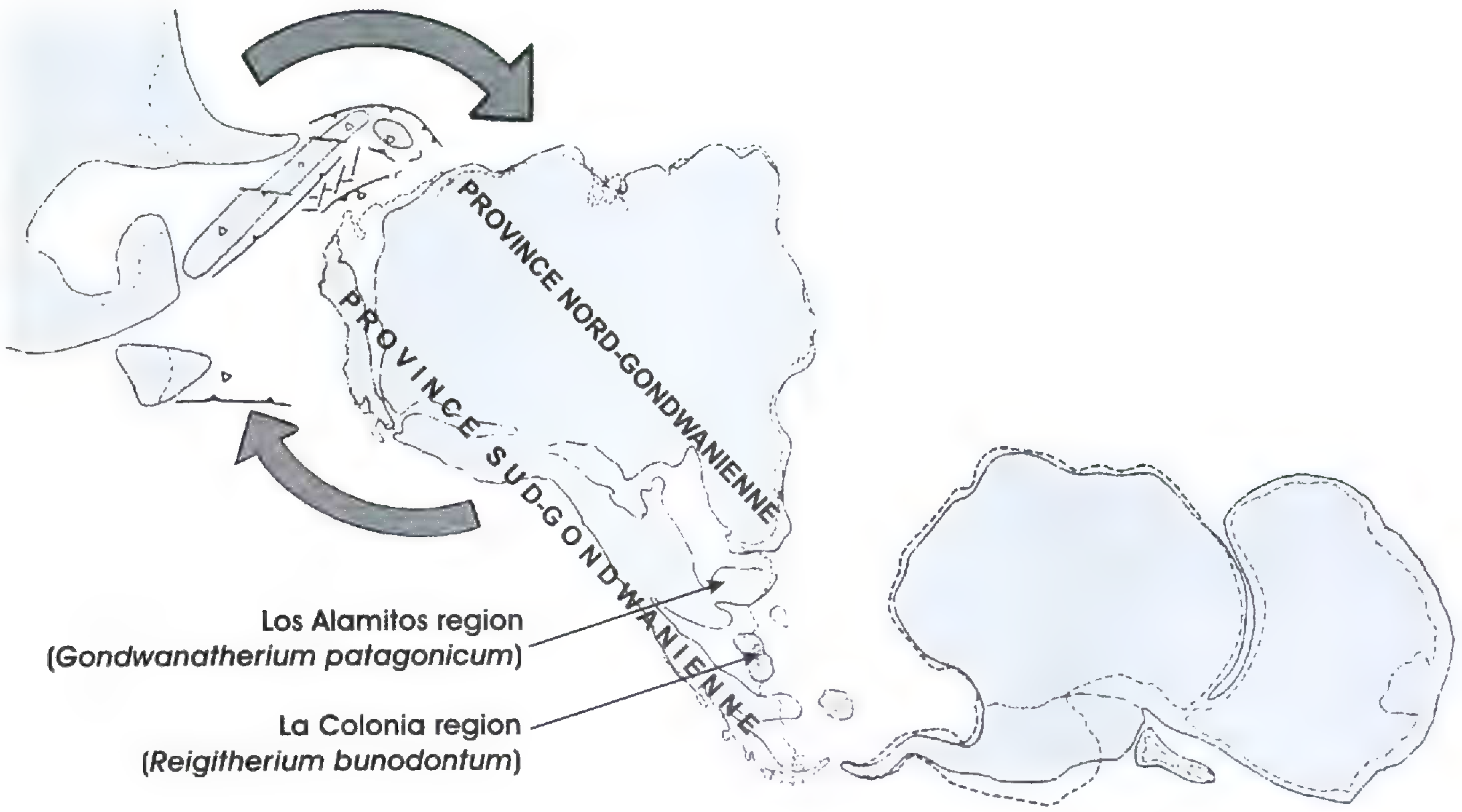

PROVINCE NORD-GONDWANIENNE
PROVINCE SUD-GONDWANIENNE
Los Alamitos region
(*Gondwanatherium patagonicum*)
La Colonia region
(*Reigitherium bunodontum*)

Figure 4. Between 85 and 63 mybP a seaway bisected the South American continent into two paleobiogeographic provinces (*fide* Broin & de la Fuente, 1993). It is likely that most of this interval was the climax of the Gondwanan Episode, and by its end the first Therian immigrants from North America inaugurated the South American Episode. Los Alamitos region and La Colonia region are the two coetaneous Campanian Patagonian localities where the two indicated Gondwanan taxa were found.

wanan survival candidates are the Xenarthra, despite the fact that none have yet been found in South American Late Cretaceous or earliest Paleocene beds.

Consequently, Simpson's (Simpson, 1950: 363) interpretation of what he termed "episodic history" of South American mammals was correct, but only applicable to the Cenozoic mammals of which he was knowledgeable.

Discussion

The best current Mesozoic record of South American land mammals is almost exclusively Patagonian and Late Cretaceous (Campanian) in age (Fig. 4). Compared to the Cenozoic record from the entire continent, the Late Cretacaeous evidence demonstrates that the entire South American land mammal history is radically divided into two major and unrelated episodes occurring under two distinct geographic sceneries. These two distinctive episodes were separated by a relatively long Maastrichtian–early Paleocene hiatus; there is only one dubious early Paleocene Patagonian specimen, a tribosphenic molar found quite recently (Goin et al., 2005). This molar may well represent one of the oldest therians to have emigrated from Laurasia, embodying the beginning of The South American Episode. Additionally, an assemblage from Bolivia, of middle Maastrichtian age based on interbedded marine taxa, includes an undoubtedly eutherian mammal, based on a molarized premolar (*non vidi*, *fide* Gayet et al., 2001). This may well represent the Ancient Immigrants from North America that inaugurated the South American Episode. We originally recognized those two major episodes as stages, plus a third, the Late Pleistocene "Neotropical Stage" (Pascual, 1996, 1998; Vizcaíno et al., 1998: 202). However, herein I recognize those two major and well distinguishable episodes as The Gondwanan Episode and The South American Episode.

The Gondwanan Episode

To date, the Gondwanan Episode is best represented by mammalian remains from two middle Patagonian localities, both Late Cretaceous in age (Los Alamitos and La Colonia, Chubut; Fig. 4). Both Patagonian Late Cretaceous mammal assemblages (apparently Campanian) are comprised only of non-tribosphenic and pre-tribosphenic mammals.

Based on the Patagonian records, and the Bolivian one (Patcha Pata) mentioned above (if the supposed eutherian is really of Gondwanan origin), The Gondwanan Episode extended from the latest Cretaceous (Campanian) to earliest Paleocene (Danian) interval, and thus far is represented only in these two central Patagonian localities, and probably Bolivia. Similar stratigraphic sequences and land mammal

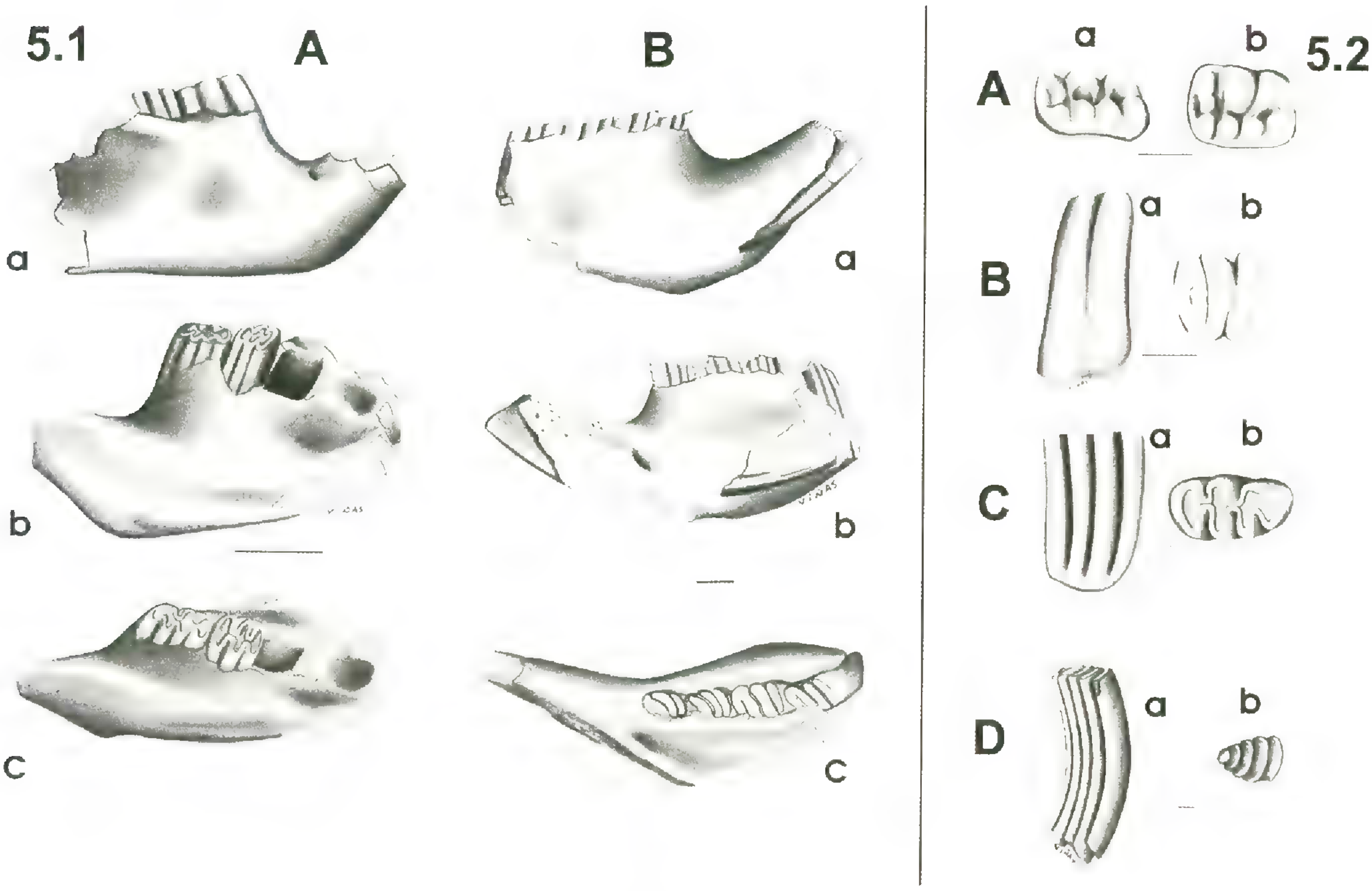


Figure 5.1. A comparison of right dentaries in (a) labial, (b) lingual, and (c) occlusal views of (A) the early Paleocene Gondwanatheria *Sudamerica ameghinoi* Scillato Yané & Pascual, 1984 with (B) the Late Miocene caviomorph rodent Dinomyidae *Tetrastylus* Ameghino, 1886 sp. Scale bars: 1 cm. Figure 5.2. A comparison of the homologous left m1 of the Gondwanatherians (A) *Ferugliotherium windhauseni* Bonaparte, (B) *Gondwanatherium patagonicum* Bonaparte, and (C) *Sudamerica ameghinoi* with the late Miocene caviomorph rodent Dinomyidae (D) *Pentastilomys* Kraglievich, 1926. Scale bars: 1 mm.

genera present at both Patagonian localities indicate synchronicity, representing continental facies of a wide-ranging epeirogenic marine Campanian-Danian transgression (Bonaparte, 1987a, 1987b, 1996; Pascual et al., 2000a; Fig. 4). This transgression extended along the length of the eastern region of the Andes, as far as the Bolivian Lake Titicaca. During the Campanian a coetaneous "Caribbean" transgression connected to the former by the Titicaca region, which, as a seaway, divided the South American territory into two Late Cretaceous–early Paleocene terrestrial biogeographical provinces ("province nord-gondwanienne" and "province sud-gondwanienne," sensu Broin & de la Fuente, 1993), verified by various abiotic and biotic evidences (Wilson & Arens, 2001; Fig. 4).

The Patagonian Late Cretaceous record (the most informative and eloquently representative base of the Gondwanan Episode) shows the total absence of tribosphenic mammals. This absence and the advanced morphology and endemism of non-tribosphenic and pre-tribosphenic mammals illustrate the most important mammalian evolutionary processes that occurred in Patagonia during the Gondwanan Episode. For example, among the non-tribosphenic taxa were the quite derived Gondwanatheria, together with dubious Laurasian Triconodonta, Symmetrodonta, and Docodonta, plus an array of quite advanced Dryolestoidea (Figs. 5, 6). The record of the Bolivian Maastrichtian Eutherian (see above) may indicate that this is not a valid generalization for the whole continent, and that Patagonia—as insinuated by some other fossil vertebrates (see below)—may have had a distinct biogeographic history, at least from the second half of the Mesozoic to the Present. In any case, this does not refute the existence of the two distinct major episodes that characterized the South American land mammal history.

Bonaparte (1988) discovered an Early Cretaceous mammal, *Vincelestes neuquenianus* Bonaparte, from another north western Patagonian locality (Fig. 3), which he considered to be Eupantotherian. To Bonaparte and Rougier (1987), Butler (1990), and Rougier et al. (1992), the level of organization of its molars appeared to be "…between the Late Jurassic *Peramus* Owen and the Early Cretaceous *Aegialodon* Kermack, Lees & Mussett" (Butler, 1990: 542). Therefore, the character states of *V. neuquenianus* placed it in an intermediate state between "non-therian" mammals and Therian taxa. Thus, Rougier (1993) grouped this advanced taxon with therians in a clade he named Prototribosphenida. Two additional

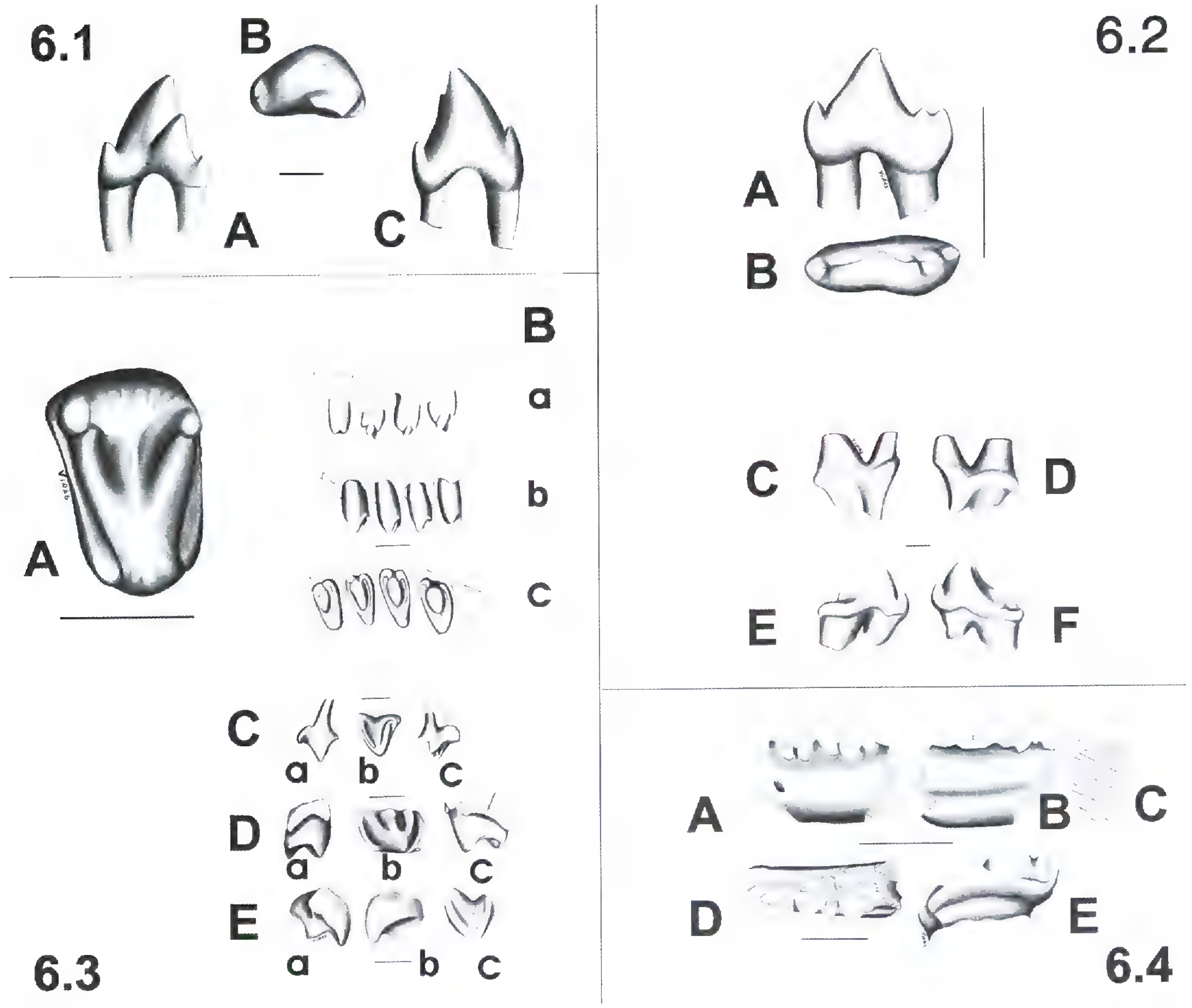


Figure 6. Upper and lower molars of the most conspicuous non-therians characteristic of the Gondwanan Episode. **6.1** Symmetrodonta. *Bondesius ferox* Bonaparte: (A) lingual, (B) occlusal, and (C) labial views of a right lower molar. **6.2.** Triconodonta. *Austrotriconodon mckennai* Bonaparte: (A) labial and (B) occlusal views of a lower molar. *Austrotriconodon sepulvedai* Bonaparte (Triconodonta?): (C) labial and (D) lingual views of a right upper molar, and (E) labial and (F) lingual views of a right lower molar. **6.3.** Dryolestoidea. Upper molars of (A) *Mesungulatum houssayi* Bonaparte & Soria, occlusal view; (B) *Leonardus cuspidatus* Bonaparte: (a) labial, (b) lingual, and (c) occlusal views; (C) *Brandonia intermedia* Bonaparte: (a) labial, (b) occlusal, and (c) lingual views; (D) *Paraungulatum rectangularis* Bonaparte: (a) distal, (b) occlusal, and (c) mesial views; (E) *Casamiquelia rionegrina* Bonaparte: (a) mesial, (b) distal, and (c) occlusal views. **6.4** Docodonta? *Reigitherium bunodontum* Bonaparte. Fragment of a left dentary: (A) labial, (B) lingual, and (D) occlusal views of premolar 1–molar 2, (C) posterior view behind molar 2, and (E) distal view of molar 2.

mammals, from two more distant Late Jurassic localities, also in Patagonia (Casamiquela, 1961; Rauhut et al., 2002; Fig. 2), as well as two Late Triassic–Early Jurassic mammal-bearing Brazilian localities (Ribeiro et al., 2001; Bonaparte et al., 2003), suggest that there were at least two more Mesozoic minor "episodes," though they are not well known to date. Supporting those Early Cretaceous and Late Jurassic minor "episodes," the paleogeographic evidence shows that these mammals evolved in different geographic situations. During the Late Triassic, what was going to be the South American continent was connected, on the one hand, to what was going to be the North American continent, and, on the other hand, to what was going to be the Gondwanan Supercontinent (*fide* Smith et al., 1994, fig. 29). By the Late Jurassic what was going to be the South American continent was already separated from what was going to be the North American continent, but still connected to Africa (Fig. 2) as part of the Gondwanan Supercontinent. By the Early Cretaceous, southern South America and Africa were already separating, with the northern sector somewhat drifted but still tenuously connected (Fig. 3; see also Storey, 1995, fig. 2c; compare these two figures with Fig. 1). The extinction of most of the Gondwanan mammals, as well as the extinction of the relictual earliest Paleocene taxa, must have occurred while the South American continent lay in the geographical position depicted in Figure 4, i.e., south of and near to the

North American continent, but still connected to the Australian continent.

The seaway mentioned above existed between ca. 80 and 64 mybP and bisected the pre-South American continent into the two biogeographic provinces, as recognized by Broin and de la Fuente (1993: 211–214) on the basis of distinct chelonian faunae: "province nord-gondwanienne" dominated by the Pelomesudae and "province sud-gondwanienne" dominated by the Chelidae. Notably, the former were, and are, well represented in the Atlantic border of equatorial Africa while the latter were, and are, common inhabitants of the Australian continent. The dipnoan fishes offer another, similar testimony: Lepidosirenidae (*Lepidosiren* Fitzinger in the province nord-gondwanienne vs. *Protopterus* Owen in intertropical Africa) and Ceratodontidae in the province sud-gondwanienne (plus *Ceratodus* Agassiz in the Late Cretaceous of Patagonia vs. *Neoceratodus* de Castelnau presently in Australia) (see Fernández et al., 1973; Pascual & Bondesio, 1976; Bondesio & Pascual, 1977).

The Late Cretaceous mammal-bearing sediments from Patagonia, representing the Gondwanan Episode, are continental facies of that southern marine seaway. The faunal biota of the province nord-gondwanienne closely resembles other Gondwanan equatorial faunal biotas, such as that from northern Africa, which, in turn, are distinct from the southern South American faunal biota that more closely resemble other austral Gondwanan faunal biotas, such as those from Antarctica and Australia (Zinsmeister, 1987; Pascual et al., 1992b, 1996). For example, the Lepidosirenidae lung-fishes during the Cretaceous were, and still are, endemic to the province nord-gondwanienne and northern Africa. This is also the case for the Chelidae turtles which are endemic to the province sud-gondwanienne and southern Africa. Similarly, the Ceratodontidae lung-fishes and the Chelidae turtles were endemic to Patagonia during the Cretaceous and are presently endemic to Australia. Crisci et al. (1991) discuss many other examples of living Insecta, Fungii, Gymnosperma, and Angiosperma, which have similar vicariant distributions in southern South America and the continents that were part of Eastern Gondwana. The hypothesis about the existence of a South American Late Cretaceous–Paleocene province nord-gondwanienne and province sud-gondwanienne was tested and confirmed by a quantitative comparison of Late Cretaceous and Paleocene palynofloras, distinct biotic elements, from austral and equatorial South American representatives (Wilson & Arens, 2001).

By the time of The Gondwanan Episode, the future South American continent was still somewhat connected to Antarctica and had drifted to just south of, and nearer to, the rising North American continent, with some archipelagic volcanic islands between each continent (Fig. 4). As a Noah's Ark (sensu McKenna, 1972), the South American Plate had been carrying relictual Gondwanan mammals. This is supported by remains from the Patagonian Los Alamitos Formation (Campanian–Maastrichtian; Bonaparte 1996), as well as those in the correlated La Colonia Formation (Pascual et al., 2000b, 2002; Figs. 5, 6). It is impossible to know when the massive extinction of Gondwanan mammals began. The separated South American continent, always situated south of the North American Plate, drifted north-northwest until the Campanian, when its mutual connection by the Panamanian "Bridge" began (cf. Figs. 2–4). As pointed out above, the complete extinction definitely occurred while the continent was already situated near to and south of the North American continent, not very far from its present position, around 80 mybP. At this time, the Caribbean sea was not yet defined, although intermediate volcanic islands enabled the first interamerican faunal exchange (Fig. 12): hadrosaurid dinosaurs from the rising North American continent and titanosaurid saltasaurine dinosaurs from the South American continent.

Closely related Gondwanatherians found in Late Cretaceous beds of Madagascar and peninsular India (Krause et al., 1997) also appear to be relictual Gondwanan mammals; they likewise survived on Noah's Ark–like continents (Fig. 7) that resulted from fragmentation of the Gondwanan Supercontinent.

THE SOUTH AMERICAN EPISODE

The last steps of The First Great Turnover (sensu Pascual et al., 2001) must have occurred during a hiatus which spanned the Maastrichtian–earliest Paleocene. This involved the extinction of all the Gondwanan mammals and their "replacement" by Laurasian therians, which emigrated from the North American sector. Apparently this marked extinction was another effect of the massive Cretaceous–Cenozoic extinction. This event marks the end of The Gondwanan Episode just as the subsequent Laurasian therian immigration marks the beginning of the South American Episode. Both episodes occurred some time during the latest Cretaceous–earliest Paleocene span, as evidenced by records in the middle Patagonian Hansen Member—usually known as Banco Negro Inferior—of the marine Salamanca Formation (early Paleocene), exposed in the coastal region of San Jorge Gulf, ca. 20 km north of Comodoro Rivadavia (Chubut) (Seillato-Yané & Pascual, 1984, 1985; Pascual et al., 1992a, 1992b, 1999; Bonaparte et al., 1993; Gelfo & Pascual, 2001; See map in Pascual et al., 1992b).

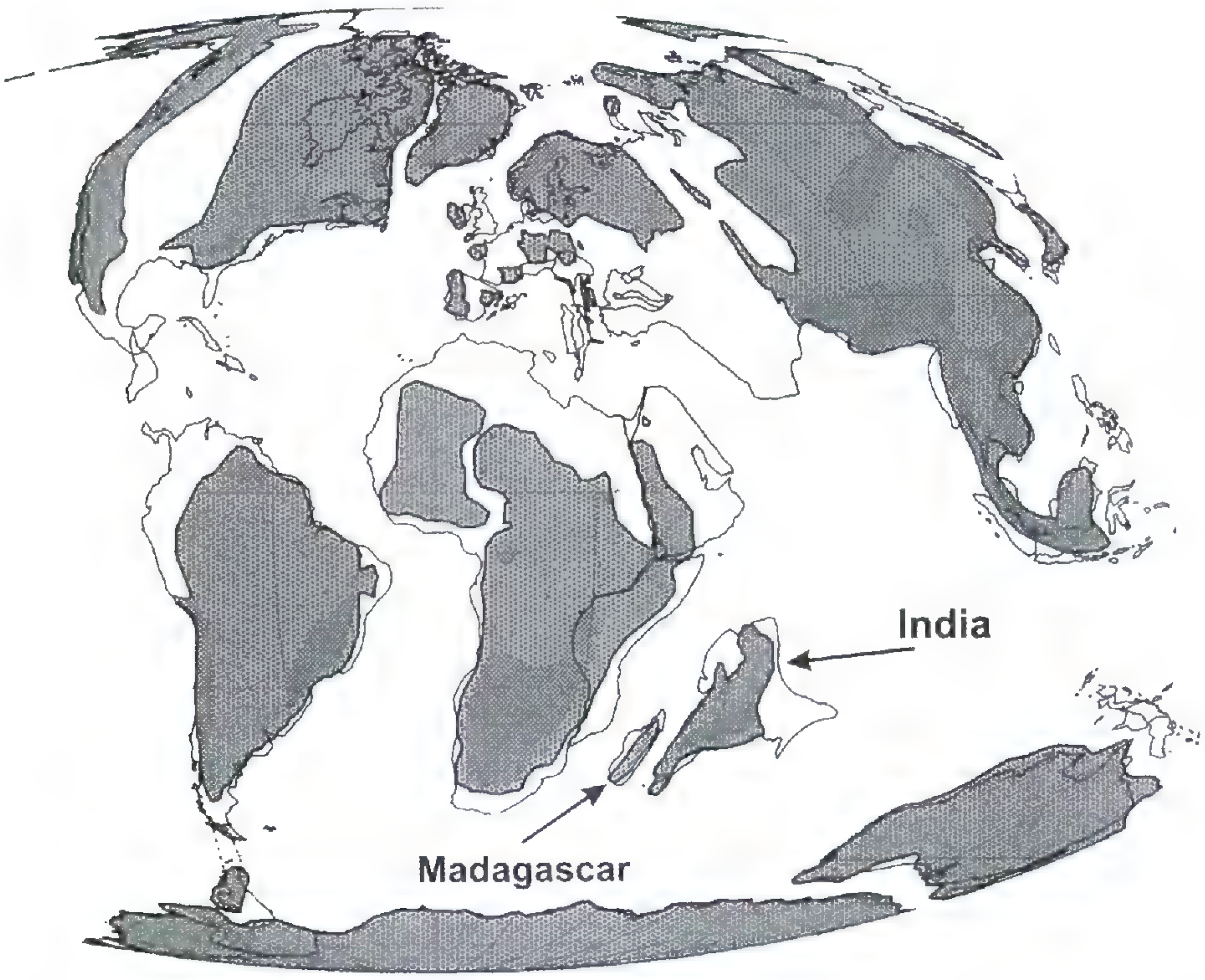


Figure 7. By aproximately 80 mybP Madagascar and India, as Noah's Ark–like continents, kept living Late Cretaceous Gondwanatherians, similar to the South American early Paleocene *Sudamerica ameghinoi*. Grey shading represents land masses 80 mybP. (Modified from Smith et al., 1994; reprinted with the permission of Cambridge University Press.)

An older Paleocene isolated, tribosphenic molar recently found by Goin et al. (Goin et al., 2005) in the Danian Lefipán Formation from central-western Patagonia appears to be the oldest known Laurasian immigrant to South America, even older than the Laurasian immigrants found in northern Bolivian beds of the Tiupampan SALMA (early Paleocene, although not earliest; see Muizon, 1991). Examples of Laurasian immigrants that inaugurated the subsequent South American Episode include the Marsupialia, Borhyaenoidea, Borhyaenidae (*Mayulestes* de Muizon), Peradectidae (*Peradectes* Matthew & Granger), Caroloameghiniidae (*Robertohoffstetteria* Marshall, de Muizon & Sige), Didelphidae (*Andinodelphis* Marshall & de Muizon, *Incadelphys* Marshall & de Muizon, *Mizquedelphy* Marshall & de Muizon, *Pucadelphis* Marshall & de Muizon, *Carolopaulacoutia* (Mckenna & Bell)(=*Sternbergia* Paula Couto), *Jaskhadelphys* Marshall & de Muizon, *Chulpasia* Crochet & Sigè, *Khasia* Marshall & de Muizon, *Sillustania* Crochet and Sige) as well as the Placentalia Leptictida (Palaeoryctidae?, cf. *Cimolestes* Marsh), Condylarthra, Hyopsodontidae (*Andinodus* de Muizon & Marshall), Mioclaenidae (*Kollpania* Marshall & de Muizon, *Molinodus* de Muizon & Marshall, *Pucanodus* de Muizon & Marshall, *Simoclaenus* de Muizon & Cifelli, *Tiuclaenus* de Muizon & Marshall), Periptichidae (*Mimamuta* Van Valen), and Pantodonta (*Alcidedorbignya inopinata* de Muizon & Marshall) (but see Bertini et al., 1993, and Gayet et al., 2001).

The tribosphenic molar from the Lefipan Formation appears to be older than the Australian and Laurasian immigrants recorded in the Patagonian Peligran Land Mammal Age beds (see Pascual et al., 1992a, 1992b; Bonaparte et al., 1993; Forasiepi & Martinelli, 2003; Pascual & Ortiz-Jaureguizar, submitted to press). These immigrants include the Platypoda, Ornithorhynchidae (*Monotrematum* Pascual, Archer, Ortiz Jaureguizar, Prado, Godthelp & Hand; Fig. 8); the Marsupialia, Didelphimorphia, Didephidae (*Derorhynchus* Paula Couto, *Didelphopsis* Paula Couto), the Polydolopimorpha, Bonapartheriidae (*Bonapartherium* Pascual), Polydolopidae gen. nov.; as well as the Placentalia, Condylarthra, Mioclaenidae (*Escribania* Bonaparte, Van Valen & Kramartz, *Raulvaccia* Bonaparte, Van Valen & Kramartz), Notopterna Notonychopidae (*Resquisia* Bonaparte and Morales).

In summary, the mammal from the Paleocene Patagonian Lefipan Formation plus the taxa from the Bolivian Tiupampan and the Patagonian Peligran appear to be among the oldest Laurasian immigrants, i.e., Simpson's (1950) Ancient Immigrants. These taxa evolved on a proto-South American substratum that included at least the Antarctic Peninsula (Fig. 8) up to about 30 mybP (Fig. 9). At the beginning of the South American Episode (early Paleocene) two Gondwanan relictual taxa, a gondwanatherian and a dryolestoid, as well as the first and unique immigrant of an Australian ornithorhynchid monotreme, persisted in central Patagonia (Fig. 8). Another relictual Gondwanan mammal was an Eocene gonwanatherian, found in the Antarctic Peninsula (Reguero et al., 2002). The Patagonian mammals of the Peligran SALMA (early Paleocene) suggest that the basic

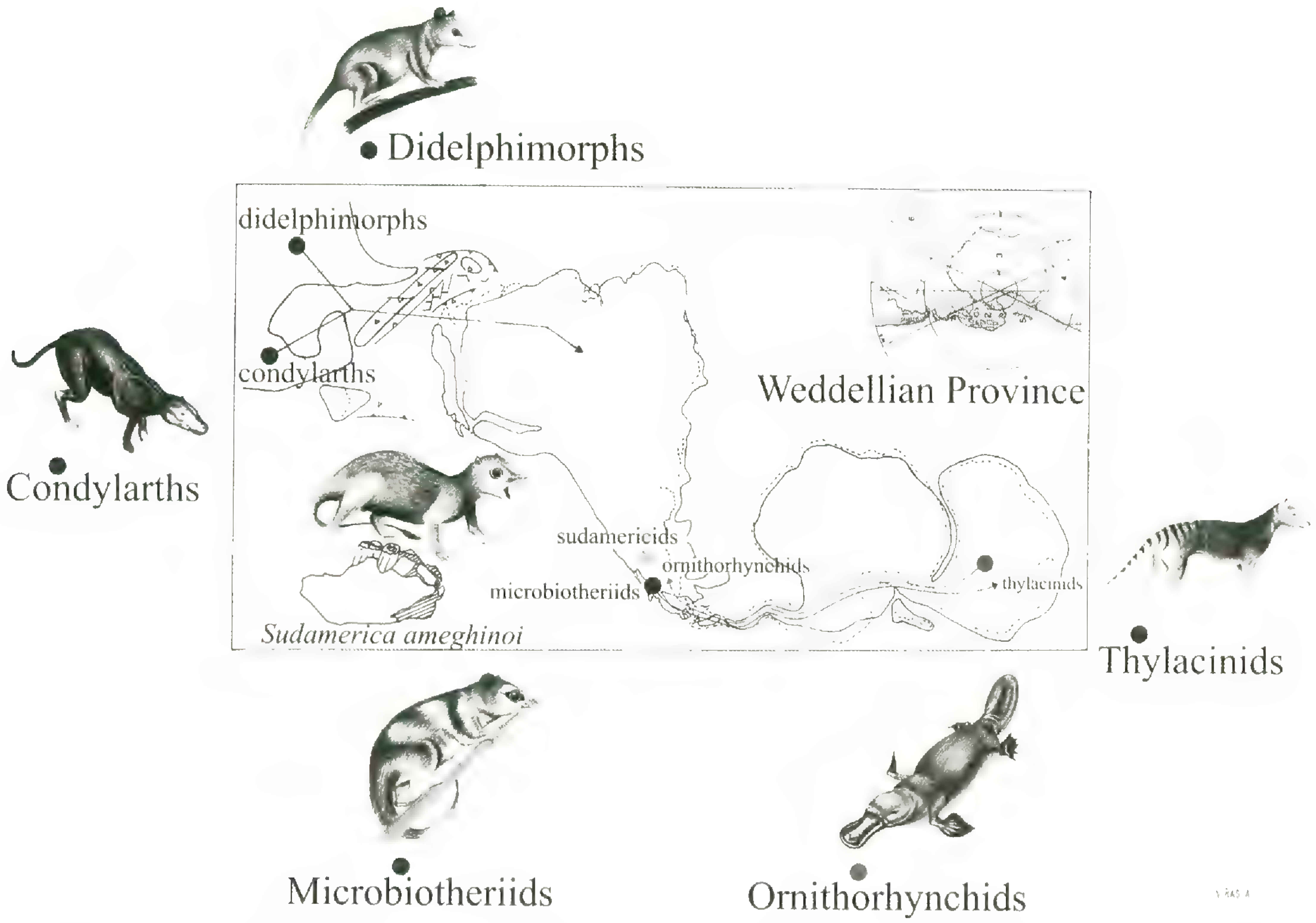


Figure 8. Inferred geographic relationships of the primordial South American continent between 85 and 63 mybP. The South American Episode began during the Late Cretaceous when the South American continent was still connected to Antarctica, i.e., not yet completely isolated. The first known immigrant tetrapod from North America was the Campanian dinosaur Hadrosauridae *Krytosaurus* Brown, 1910 sp. Probably by the Late Cretaceous, and certainly by the early Paleocene, it was followed by Metatherian and Eutherian mammals, ancestors of the taxa depicted here. However, their immigration may have begun by the pre-Campanian Late Cretaceous. By the Late Cretaceous, marsupials emigrated to Australia and, following the same route, by the early Paleocene, South America received the first Australian immigrant, the monotreme ornithorhynchid *Monotrematum sudamericanum* Pascual, Archer, Ortiz Jaureguizar, Prado, Godthelp & Hand, 1992b. Dark grey bullets and arrow indicate the first immigrants from North America to South America. Among them the microbiotheriids were the first marsupials to emigrate from South America to Australia, through the Antarctic continent. Thylacinids are one of the end products differentiated in Australia from South American marsupials (Sparassodonta?). *Sudamerica ameghinoi* Scillato Yané & Pascual, 1984 is the first and last Gondwanatheria found in Late Cretaceous and early Paleocene beds from Patagonia. Ornithorhynchids are the first monotreme found outside (Late Cretaceous–early Paleocene of Patagonia) of Australasia.

diversification of the immigrant therians was well on its way. If those therian mammals recorded by Bertini et al. (1993) and Gayet et al. (2001) really were of Late Cretaceous age and immigrants from Laurasia (North America), then they are the oldest known immigrants, i.e., Simpson's (1950) Ancient Immigrants.

In accordance with the main turnovers withstood by the Cenozoic land-mammal communities, otherwise related to first order diastrophic and climatic phenomena, it is clear that four main stages of the South American episode can be recognized:

(1) The span between the extinction of the last Gondwanan land mammals and the very first immigration of the Laurasian Marsupialia and Placentalia (in part contemporaneous) as well as the late Eocene–early Oligocene immigration to South America of primates and rodents (apparently from Africa; Fig. 10). This interval corresponds to what we have distinguished as the "most autochthonous part of the history" (Pascual et al., 1985: 230–231; Figs. 9, 10), during which the basic diversification of the South American mammals occurred. This event also comprised the Protocenozoic and Infracenozoic Supercycles, which probably extended back to include the last part of the long Patagonian sterile Maastrichtian–earliest Danian span.

(2) The end of the Infracenozoic Supercycle led to the beginning of a new evolutionary cycle, marked by the late Eocene–early Oligocene Turnover (also known as La Grande Coupure or the Terminal Eocene Event). The archaic lineages of ungulate mammals (brachydonts) that had gradually changed from protohypsodont (Eopatagonian Cycle) to almost eu-

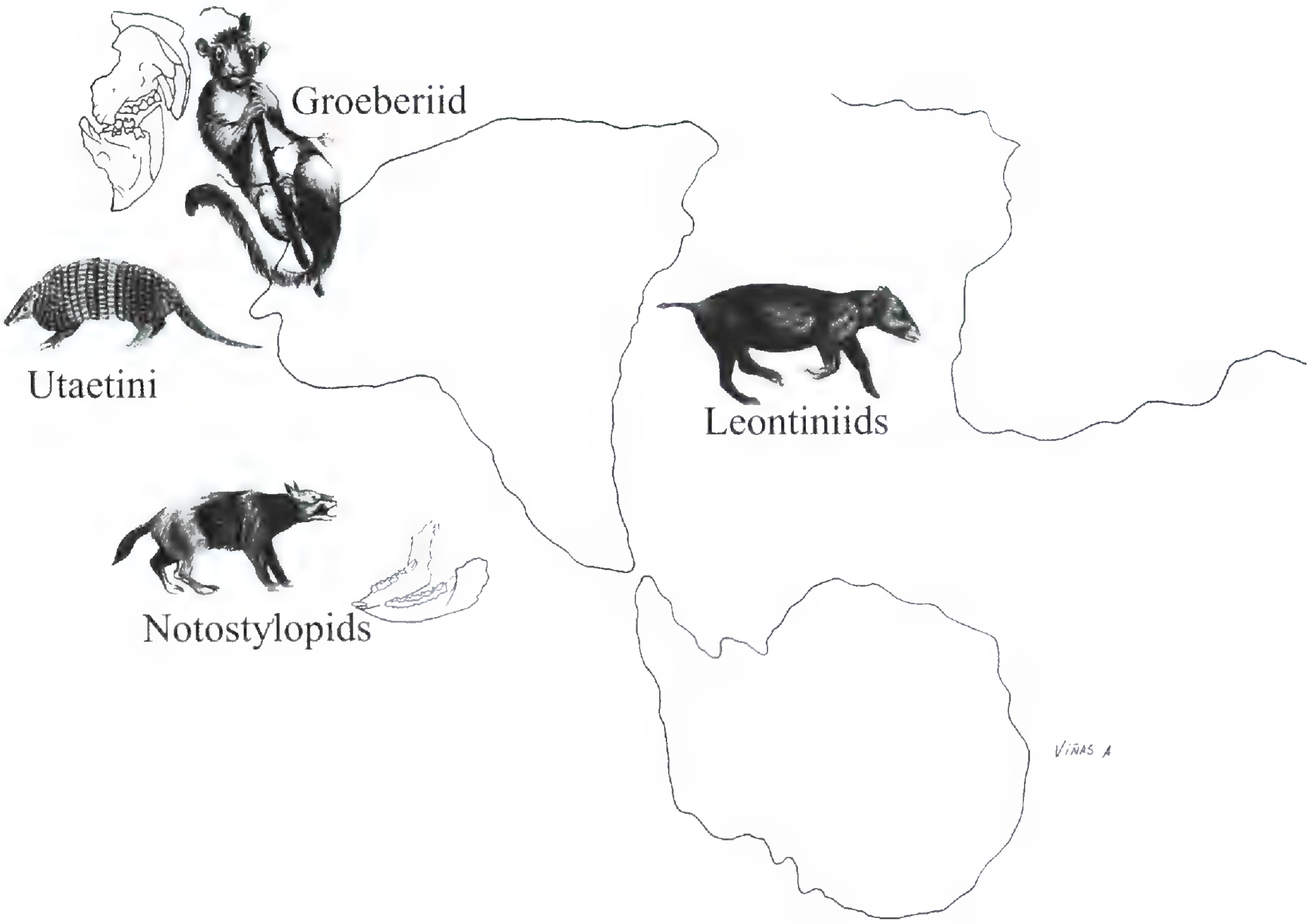
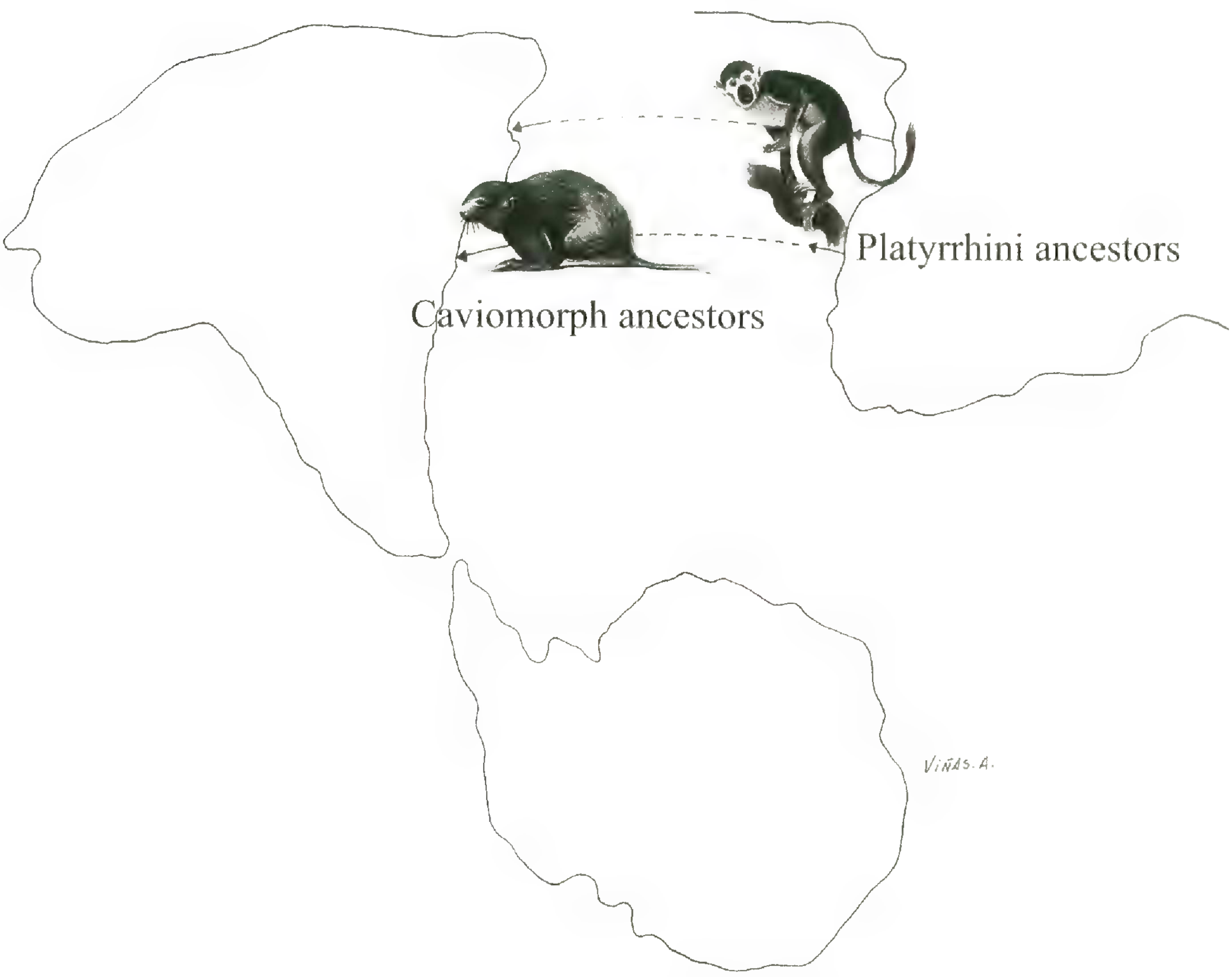


Figure 9. By the late Eocene (ca. 30 mybP) the South American continent was isolated. During the Eocene, the immigrant Therians had differentiated into the most advanced and varied lineages of mammals, e.g., the marsupial Groeberiid, the xenarthran dasypodids, Utaetini, and the notoungulates, Notostylopids, and Leontiniids. We recognized this interval as the most autochthonous part of the South American mammalian history.

hypsodont types (sensu Mones, 1979, 1982) (Prepatagonian Cycle), was replaced by a quite modern stamp of native ungulates (euhypsodont), which characterized most of the native ungulates of the Patagonian Cycle and all subsequent cycles up to the end of the Pleistocene (Panaraucanian and Pampampean Cycles; Table 1). We qualified the beginning of this process (i.e., the Patagonian Cycle) as "The First Major Change Toward a Modernization" (Pascual et al., 1985: 232–234). At this point, the history of South American mammals passed from "Early Experimentation to Modern Standardization" (*fide* Gould, 1983: 21). This turnover appears to be regionally connected to climatic and/or environmental changes, related to a series of geotectonic phenomena, e.g., the diastrophic Inca Phase, and quite possibly also the Pehuenche Phase (see Tertiary Andine Diastrophism in Table 1), the completion of the Drake Passage, and the consequent separation of South America from Antarctica as an island continent (Fig. 10), with all the climatic consequences derived from the formation of the encircling Antarctic Current.

Thus, the evolutionary processes leading to the differentiation of the unique South American land mammals, until ca. 30 mybP, also had the Antarctic Peninsula, and probably some other portion of the Antarctic continent, as substratum. Simpson's (1950) Ancient Immigrants developed on this scenery. Simpson's two other episodes (Faunal Strata in a figurative sense), which he named Old Island Hoppers and Late (Island Hoppers and) Immigrants (Simpson, 1950: 364), respectively, developed while the continent was isolated, except toward the end when the inter-American terrestrial connection began with the newborn Panamanian Land Bridge (ca. 2.5 mybP), and through it the terrestrial transit (i.e., walking) of what Stehlin and Webb (1985) termed The Great American Biotic Interchange. During the isolation period preceding this interchange the modernization of the native mammals increased, particularly manifested in the augmentation of hypsodontism of the herbivore grazers among the native placental mammals, as well as in some peculiar marsupials, such as the Argyrolagidae (*Proargyrolagus* Wolff) and the Patagoniidae (*Patagonia* Pascual and Carlini). Two main subcycles characterize this interval (Pascual et al., 1985): the Deseadan Subcycle and the Pan-Santacrucian Subcycle.



INFRACENOZOIC SUPERCYCLE

OLD ISLAND HOPPERS

Figure 10. Approximately coincident with the separation of the South American and Antarctic continents (ca. 30 mybP), rodents (non-cricetids) and primates immigrated from Africa by sea.

During the Deseadan Subcycle (late Oligocene–earliest Miocene), according to the Patagonian record, over the southern extreme of the continent the most primitive Paleogene mammals vanished or disappeared and some very important cladogenetic processes came to an end, especially within very diverse lineages. On the other hand, from small contemporaneous mammals related to the latter, new cladogenetic processes began. For example, certain notoungulates evinced the precocious acquisition of high-crowned teeth, and caviomorph rodents were recorded for the first time at austral latitudes (see Patterson & Pascual, 1972; Pascual et al., 1985, and literature therein). According to Zachos et al. (2001), this cycle occurred between two glaciations, known as Glaciation Oi-1 and Glaciation Mi-1, which developed in Antarctica and the southernmost part of the South American continent. Furthermore, also according to Zachos et al. (2001), completion of the Drake Passage occurred in between these two glaciations (Table 1), i.e., around 30 mybP.

The following Pan-Santacrucian Subcycle represents the southernmost record of any of the South American SALMAs. Apparently related to the end of the Mi-1 Glaciation, a change to relatively mild conditions occurred. These mild conditions culminated about 15 mybP, with the so-called Mid-Miocene Climatic Optimum, and correspond to the time that preceded the Quechua Phase of the Tertiary Andean Diastrophism. Considering the entire fauna, Webb (1978) remarked that its rich diversity of medium to large-sized mammals strongly infers a broad environmental impact, i.e., an optimum balance between grasslands and woodlands provided by savanna. An intense drop in sea level ca. 30 mybP occurred due to glaciation, followed by intermittent drops in sea levels culminating with the Plio–Pleistocene glaciations (Table 1). Around 18 mybP the first emigration of native South American land mammals occurred, although not to North America but to the West Indies. Around that time, caviomorph rodents and megalonychid xenarthrans (Fig. 11) and probably also the

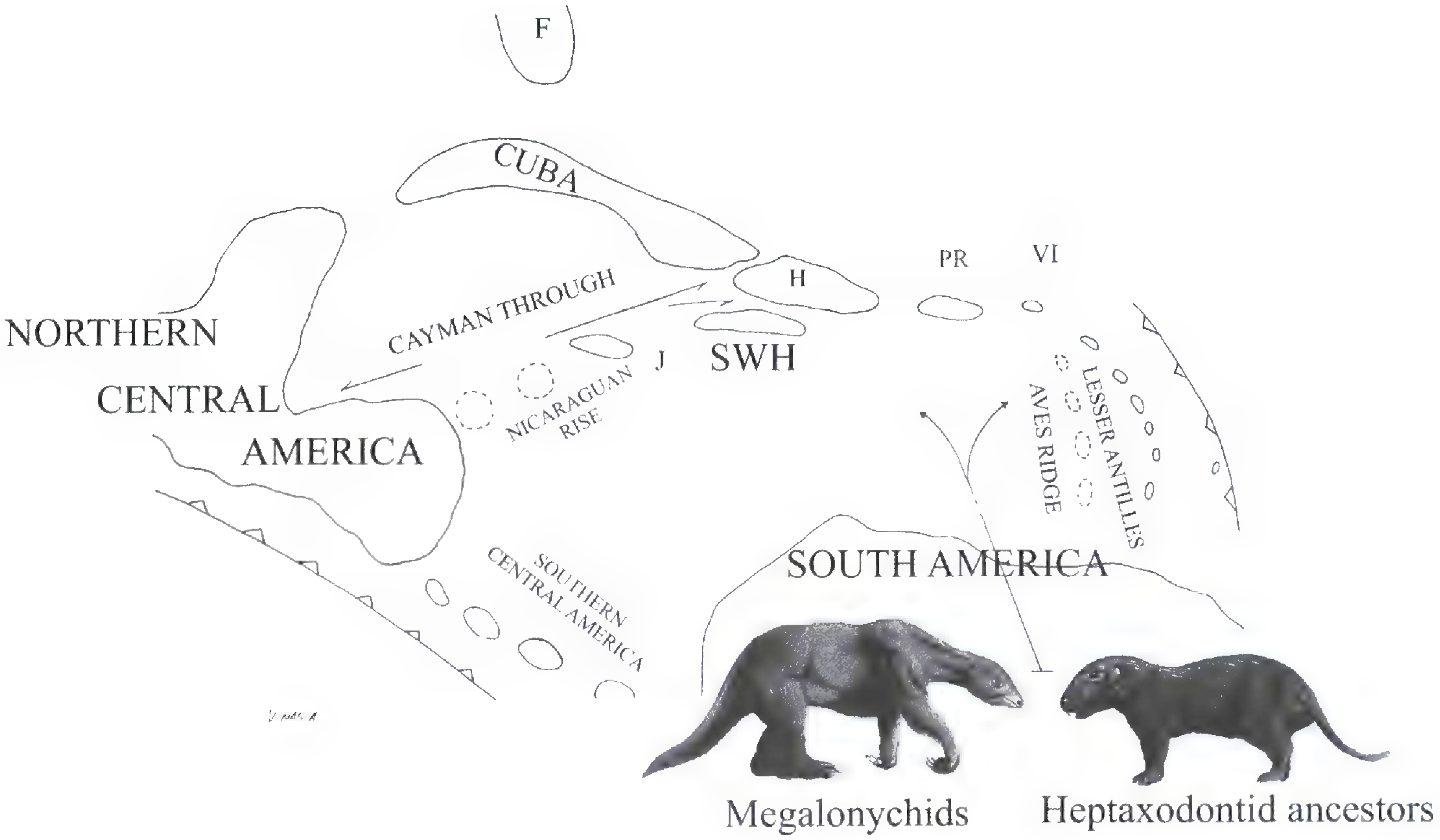


Figure 11. By 18 mybP the first dispersal event of South American mammals occurred: Xenarthran Megalonychids and Dinomyid rodents emigrated (as island-hoppers) to the West Indies.

platyrrhine primates—populated the Antilles, most likely as island-hoppers. There they underwent a notable evolutionary radiation. The megalonychid xenarthrans, the heptaxodontid rodents, and the platyrrhine primates became extinct quite recently, within historical times, while the capromyid rodents are extant. These are regional descendants of those South American immigrants, or probable vicariant taxa according to MacPhee & Iturralde-Vinent (1994). Curiously, both the megalonychid xenarthran and the heptaxodontid rodents differentiated into some peculiar ecological types, including tree-sloth-like forms (Matthew & Paula Couto, 1959; Paula Couto, 1967; Pascual et al., 1990) and cursorial, elasmodont heptaxodontid rodents very similar to the Miocene South American phoberomyine neoepiblemids and eumegamyine dinomyids (Pascual et al., 1990). Among the West Indies rodents, all those with elasmodont molariform dentition have been lumped into a single family, Heptaxodontidae, although sometimes with hesitation (e.g., Ray, 1964). Nevertheless it is suggestive that the peculiar Jamaican *Clidomys* Anthony, 1920 (see MacPhee et al., 1983; MacPhee, 1984) is very similar to the South American Neoepiblemidae in dental structure. On the other hand, the remaining Heptaxodontidae are more similar to the highly diversified Dinomyidae. This difference may indicate that there was more than one immigratory event of rodents (Fig. 11).

The following Pan-Araucanian Cycle, as we called it (Pascual et al., 1985), was with the diastrophic Quechua Phase, known by most geologists as the orographic phase (e.g., Vicente, 1972). The elevation of the Andes displaced the most propitious environments for land mammals to both sides of the cordillera (Ortiz-Jaureguizar et al., 1993). On the eastern sector of the rising Andes, extensive plains arose, first comprised of pyroclastic mammal-bearing sediments, and then clastic sediments; the middle pampas region also had an important component of pyroclastic sediments.

Mammals on opposite sides of the cordillera had long been considered as representing two distinct and successive ages (e.g., Marshall & Salinas, 1990). On the basis of a multivariate analysis, Ortiz-Jaureguizar et al. (1993) suggested that they are correlative and proposed that both be maintained under the original name of the Friasian SALMA. The Frias Formation, both in Patagonia and in extra-Patagonian regions of Argentina, was deposited under the influence of the withdrawal of an extensive middle Miocene marine transgression. We (Pascual et al., 1996: 291) made the interpretation that the distinction of the Friasian land mammals with respect to the preceding subtropical Santacrucian one was related to the climatic and environmental effects of the first subphase of the complex Quechua orographic phase, as well as to the global climatic changes, as evidenced by the

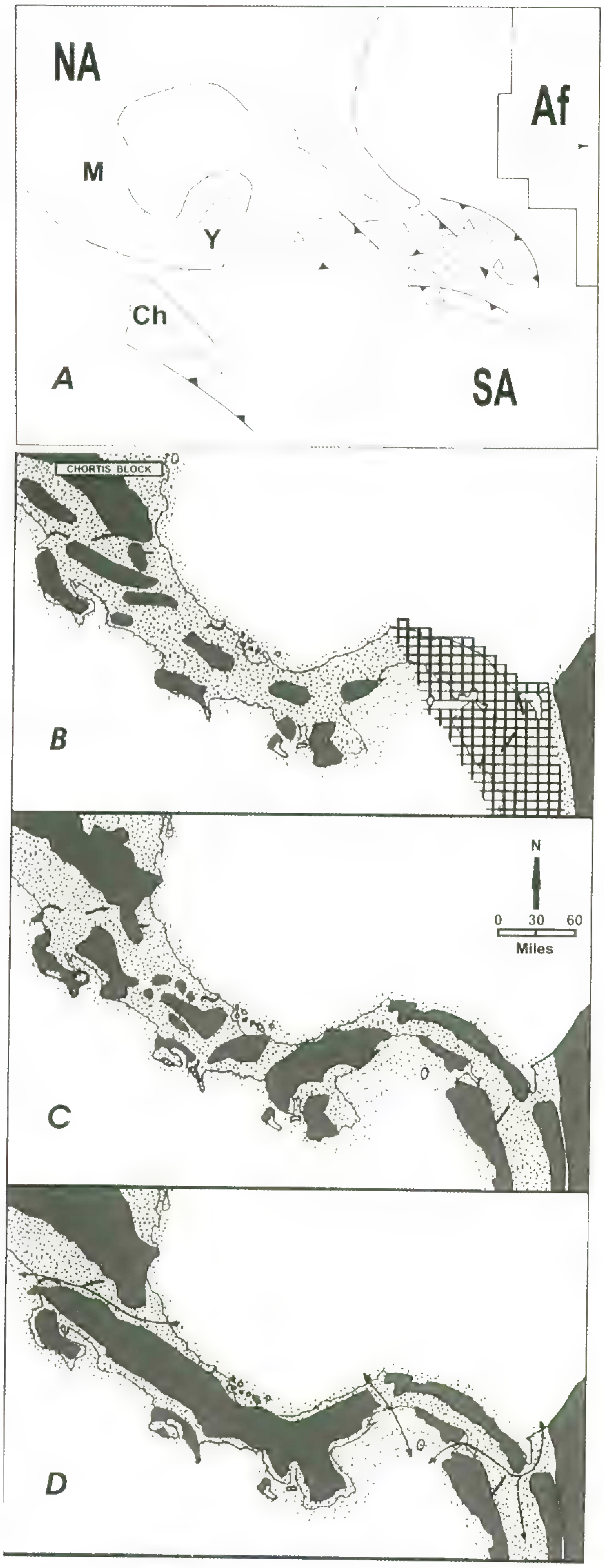


Figure 12. The rising Panamanian land bridge established a definitive connection between North and South America. —A. By 85 mybP the interamerican "exchange" of terrestrial tetrapods began: hadrosaur dinosaurs from North America and titanosaur saltasaurines from South America. Apparently this occurred through some kind of land bridge (archipelagic) related to Donnelly's (1973, 1985) Flood Basalt Episode. **M** = Mexican block; **Y** = Yucatán block; **Ch** = Chortis block. (A modified from Donnelly, 1985, with permission of Springer Science and Business Media.) —**B.**

←

About 15–16 mybP, the present Panamanian Land Bridge was occupied by an abyssal sea more than 2000 meters deep. —**C.** Some time before 7 mybP the Caribbean region began to be built up and the "Island Hoppers" interchange (Simpson, 1950) began. —**D.** Between 2.5 and 3 mybP the terrestrial inter-American connection was almost completed and, consequently, the formation of the present American Atlantic coast was also almost complete. This, and the subsequent final connection, began the massive interchange of terrestrial mammals, i.e., Simpson's "Late (Island Hoppers and) Immigrants." (A. Dotted lines indicate the present geographical limits; open triangles: calc-alkaline volcanism; closed triangles: subduction and island-arc or continental-margin magmatism around the Caribbean. B–D. Grey shading: continental blocks; dotted areas: shallow marine environments; grids: deep marine (> 2000 m) environments. D. Lines with arrows: seaway.) (B, C, and D reprinted from *Paseo Pantera: Una Historia de la Naturaleza y Cultura de Centroamerica* by Anthony G. Coates (Washington, DC: Smithsonian Books). Used by permission of the Smithsonian Institution. Copyright 2003.)

relatively sudden divergence between high and low latitude marine temperatures. According to Savin and Stehli (1975), high-latitude temperatures dropped dramatically, but low-latitude temperatures remained constant or even perhaps increased. In a period probably not exceeding 2 to 3 million years, minimum temperatures appear to have dropped 3°C, or at a rate of about 1°C per My. Based on fossil land mammals and other tetrapods, the wide-ranging plains that built up on the eastern slopes of the Andes became successively more and more arid to the west, with more humid portions to the northeast influenced by the humid Atlantic winds. The successive sedimentologic mammal-bearing units deposited toward the northeast part of Patagonia (Chasicoan, Huayquerian, Montehermosan, and Chapadmalalan SALMAs) progressively contain a notable increase in North American immigrants corresponding with a change toward finest granulometric sediments (silty–loessoid), as well as with the pace that the Panamanian land bridge was being built up.

Contrary to the increasing trend of eupsydontism in the native ungulates, the immigrant ungulates were brachydont, or at the most mesodont. The withdrawal of the Miocene marine transgression was succeeded by a period of similarly widespread and varied plains that we distinguished as the "edad de las planicies australes" (Pascual & Bondesio, 1982: 29). In such a way the late Miocene–Pleistocene pampas of present times initiated their differentiation. Mammal-bearing sediments, with good ecological indicators, clearly show the north-northeast environmental displacement. At the beginning, i.e., during the middle Miocene, the last appearances of some Santacrucian mammals are recorded (Pascual et al., 1965: 177). In general, and in accordance with the

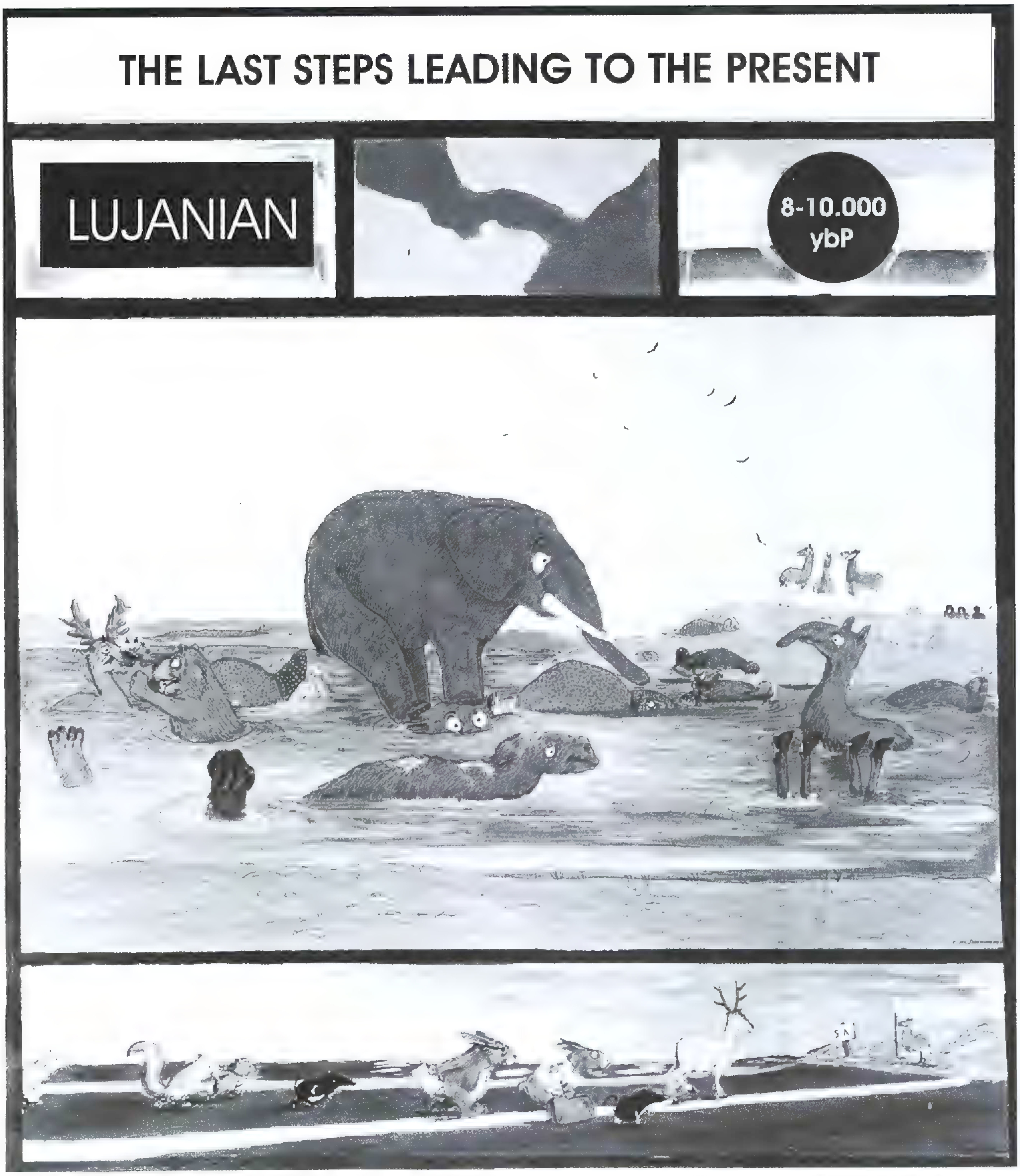

THE LAST STEPS LEADING TO THE PRESENT
LUJANIAN
8-10.000 ybP

Figure 13. About 8000–10,000 ybP the "Megafaunal Extinction" and subsequent newcomers began to feature in the modern Neotropical mammal assemblage.

fossil record, the abundance of native ungulate herbivores was markedly reduced, accompanied by a great increase in the numbers of such specialized herbivores as huge edentates and caviomorph rodents. It is important to emphasize that there was a successive gradual increase in immigrants of North American origin toward the end of the Miocene, from the Late Island-hoppers to the early walkers, through the rising Panamanian Bridge, i.e., Simpson's (1950) Late (Island Hoppers and) Immigrants (cf. Fig. 12 B–D). Within the temperate regions of the continent, forest progressively declined and was replaced by extensive grasslands. As a consequence, cursorial and grazing native communities of mammals spread, setting the stage for the forerunners of the pampean's (late Pliocene–Pleistocene) peculiar inhabitants.

(3) The third stage is marked by the beginning of the interamerican exchange of land mammals, which prima facie is related to the beginning of the land connection between the Americas, in part due to the sustained low sea level that followed the Quechua Phase (Table 1, Eustatic Curve). As a consequence, a notable increase of North American immigrants occurred; the supposedly strong influence of these immigrants on the extinction of native mammals has been strongly disputed (e.g., Patterson & Pascual,

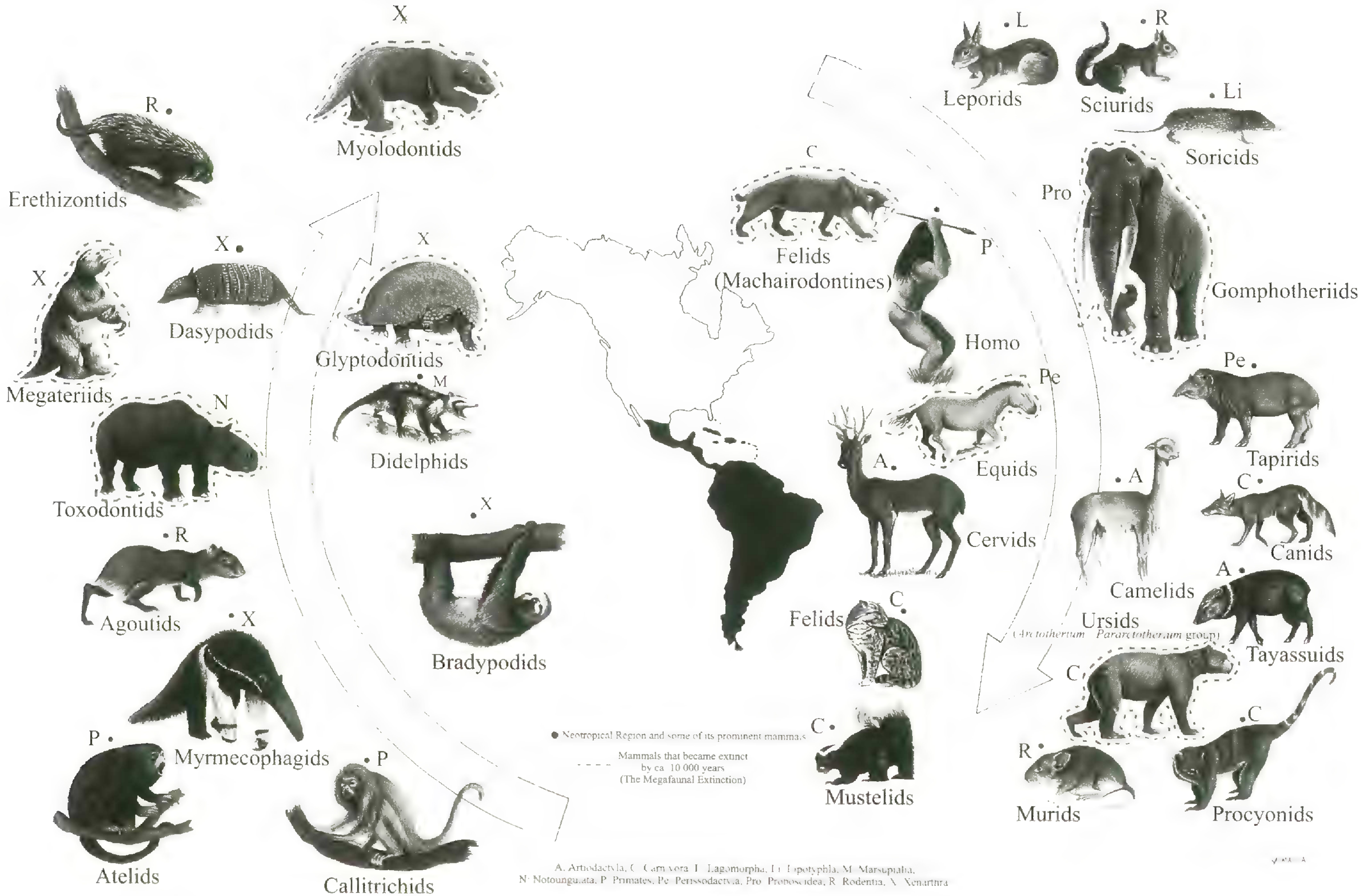

X
Myolodontids
R
Erethizontids
X
Megateriids
X
Dasypodids
X
Glyptodontids
M
Didelphids
N
Toxodontids
R
Agoutids
X
Bradypodids
X
Myrmecophagids
P
Atelids
P
Callitrichids
L
Leporids
R
Sciurids
Li
Soricids
Pro
Gomphotheriids
C
Felids (Machairodontines)
P
Homo
Pe
Equids
A
Cervids
Pe
Tapirids
A
Camelids
C
Canids
A
Tayassuids
C
Felids
Ursids (Arctotherium Pararctotherium group)
C
C
Procyonids
C
Mustelids
R
Murids
Neotropical Region and some of its prominent mammals
Mammals that became extinct by ca. 10 000 years (The Megafaunal Extinction)
A. Artiodactyla, C. Carnivora, L. Lagomorpha, Li. Lipotyphla, M. Marsupialia,
N. Notoungulata, P. Primates, Pe. Perissodactyla, Pro. Proboscidea, R. Rodentia, X. Xenarthra

Figure 11. Between 2.5 and 3 mybP the principal interchange of the Great American Biotic Interchange (Stehli & Webb, 1985), whose acme was about 1.5 mybP, began. "The predominance of savanna-adapted mammals indicates a continuous corridor of such vegetational formations as thorn scrub or seasonally arid woodland, whereas they are now separated by at least 1700 km of humid tropical forest. . . The final link between American mesic equatorial biotas evidently was established in the late Pleistocene" (Webb, 1985: 381). The fates of mammals that participated in the Great American Biotic Interchange, up to the present Neotropical Region, are indicated on each of the most representative selected taxa depicted here.

1972; Cifelli, 1985). During the 5th International Theriological Congress in Rome (1989), Ortiz-Jaureguizar (1989: 277–278), Goin (1989: 271–272), and Tonni et al. (1989: 285–286), among others, again questioned the competitive model for extinction of the South American latest Pleistocene mammals.

There is hard evidence that some South American megalonychid and mylodontid xenarthrans (Webb's (1985: 358–359) "heralds of the South"), and apparently some North American carnivores such as the procyonids, were able to cross the marine barriers from about 8 to about 9 mybP, i.e., more than 5 Ma before the completion of the Panamanian land bridge, estimated at 2.5–3 mybP (Fig. 12). These taxa were among Simpson's Late Island Hoppers. Thus, the final terrestrial connection of the Americas by the newly built Panamanian bridge initiated the massive inter-american exchange, whose acme occurred by the Ensenadan SALMA, between 1.8 mybP and ca. 60,000 ybP (Cione & Tonni, 1995, 2001). This occurred concomitantly with a progressive extinction of most of the native mammals, culminating in what has been called "The Megafaunal Extinction" by Martin (1984: 355; see figures encircled on Fig. 14), which was an extinction phenomenon that, with some temporal differences, occurred almost all over the world.

(4) The last and fourth stage that marks the history of South American mammals is the so-called "Megafaunal Extinction" (Fig. 13). This is an extraordinary event that took place about 10,000 years ago. Together with the preceding arrival of man about 13,000 years ago, this event shaped the basic mammalian fauna of the present Neotropical Region (see representative taxa with bullets in Fig. 14). Simultaneously or somewhat later, i.e., in post-Pleistocene times, the last North American immigrants (quite probably inhabitants of Central America) arrived. These included rodents such as Heteromyidae, Geomyidae, and Sciuridae; Lagomorpha such as Leporidae; and Insectivora such as Soricidae. Also included were some genera of families already living in South America, such as the cervid *Odocoileus* Rafinesque (see the lower part of Fig. 13).[3]

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[3] Exhaustive details related to the integrated geobiotic phenomena that led to The Great American Biotic Interchange can be found not only in this Symposium, particularly in the paper by S. D. Webb, but also in the 1985 book *The Great American Biotic Interchange*, Stehli and Webb (editors); *Late Cenozoic Mammals*, Symposium 9 of the 5th International Theriological Congress in Rome, R. Pascual and S. D. Webb (editors), 5th ITC, Rome, 1989, Abstract of Papers and Posters, Vol. 1, pp. 260–291; Chapters 1, 2, 4, and 5 of the 2003 book *Paseo Pantera: Una Historia de la Naturaleza y Cultura de Centroamérica*, A. G. Coates (editor), Smithsonian Institution Press, Washington D.C. and London; the 1996 book *Evolution and Environment in Tropical America*, J. B. C. Jackson, A. F. Budd, and A. G. Coates (editors), The University of Chicago Press; and the 1999 book *A Paleobiotic Survey of Caribbean Faunas from the Neogene of the Isthmus of Panama*, L. S. Collins and A. G. Coates (editors), Bull. Amer. Paleontol. 357.

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